BEHAVIOURAL ECOLOGY OF WESTERN LOWLAND GORILLAS IN GABON

Elizabeth Ann Williamson

Thesis submitted for the degree of Ph.D

University of Stirling

1988

ABSTRACT

The behavioural ecology of western lowland gorillas was studied for 16 months in the Lope Reserve, Gabon, where gorillas are sympatric with chimpanzees in lowland tropical forest. Data were collected by direct observation, and by examination of nest-sites, feeding-sites, and trails. The nature of frugivory and the extent of seasonal variation in food selection were emphasised. Dietary composition was identified, and the contribution of fruits was evaluated from the volume of fruit ingested, estimated retrospectively from seeds in the gorillas' dung.

Forest structure and composition were assessed using transects, and fruit and leaf production was quantified monthly to estimate food availability. Food distribution was patchy, and many foods showed seasonal peaks in adundance.

The heterogeneity of the habitat was reflected in the diverse diet: gorillas ate 139 parts of 103 species of plants, including 78 fruits. One third of dung samples contained weaver ants. Vegetative parts of Aframomum and Marantaceae formed staple foods, due to their abundance, accessibility, and year-round availability. Succulent fruit formed over 90% of fruit intake. Seasonal variation was measured in all dietary parameters. Flexible foraging strategies enabled gorillas to cope with fruit scarcity, particularly during the major dry season: when less fruit was available gorillas consumed more stems, leaves, and bark, and ate poorer-quality fibrous fruits.

Ranging was influenced by the seasonal availability of particular food species: when fruit was abundant gorillas travelled large distances between sources, when scarce they adopted a low-cost strategy, shifting their diet to wards more abundant, but poorer quality foods, and travelling less.

Differences in feeding, ranging, and climbing between lowland and mountain gorillas result from striking differences in their respective habitats, especially in the abundance and distribution of fruit sources. Lowland gorillas' home ranges were larger; they spent more time in trees, mostly feeding; yet their social structure seemed to be similar to mountain gorillas'.

Lope gorillas adopted strategies similar to those of other frugivorous primates: fruits were preferred foods, consumed with fibre and leaves to meet nutritional requirements. The switch in diet was faciliated by the gorillas' large body-size, which may have enabled them to cope with succulent fruit shortages, and allowed gorillas to remain in relatively stable groups.

ACKNOWLEDGEMENTS

First, I gratefully acknowledge the bodies who funded this research: The Boise Fund, the L.S.B. Leakey Foundation, the L.S.B. Leakey Trust, Stirlingshire Educational Trust, the University of Stirling, and the Wenner-Gren Foundation for Anthropological Research.

For permission to work in the Lope Reserve I thank M. Raphael Dipouma, the Directeur de la Chasse et de la Faune, Ministere des Eaux et Forests in Gabon.

Dr. Caroline Tutin and Michel Fernandez provided the opportunity to live and work in the Lope Reserve. I am very grateful for their hospitality and for use of the facilities at the Station d'Etudes des Gorilles et des Chimpanzes.

Dr. David Newbery helped greatly with analysis of the vegetation data. Simon Booth, of the Computer Unit at Stirling University, enabled me to carry out manipulations of the data successfully, Nan Hutcheon entered most of the data into the computer, and Sue Williamson helped to type the references. I am also grateful to F.N. Hepper and the Royal Botanic Gardens at Kew, Dr. Annette Hladik, and Nicholas Halle for identifying plant specimens.

For contributing to the data presented in this thesis I thank Dr. Jean-Yves Collet, Jean-Paul and Chantal Coupin, Anna Feistner, Michel Fernandez, Dr. Mike Harrison, Dr. Bill McGrew, Ann Pierce and Dr. Liz Rogers, but mostly I thank Dr. Caroline Tutin.

For guidance and encouragement in the field I thank Caroline and Michel, and for the same at Stirling I am indebted to Bill McGrew and Arnold Chamove. Bill McGrew, Arnold Chamove, Anna Feistner and Mike Harrison provided constructive criticism of the manuscript. For general support and practical help in the production of this thesis I am grateful to the above, together with Alyn Brereton, Alison Hannah and Eluned Price. I also thank Drs. Sian Evans and Bob Cooper for their hospitality at Franceville.

There are many people who helped me to complete this research, and whose love and support were invaluable both in Gabon and in Stirling, especially Charles and Barbara Williamson, my parents, and Susan, my sister. I thank Kathleen Ryall for being so tolerant and supportive during the last two years. And I acknowledge Patrick Candler for his unique forms of support.

Last, I am indebted to my superviser, Dr. Bill McGrew. Few people would have provided such constant encouragement, support and advice. Without him this thesis would have been neither started nor completed.

CONTENTS

CHAPTER 1: INTRODUCTION

CHAPTER 2: METHODS

CHAPTER 3: VEGETATION

CHAPTER 4 : FEEDING

CHAPTER 5: NESTS AND NESTING

CHAPTER 6: SOCIOECOLOGY

CHAPTER 7 : GORILLAS' RESPONSES TO OBSERVERS

CHAPTER 8: DISCUSSION

CHAPTER 1: INTRODUCTION

A. HISTORICAL PERSPECTIVE

"They sleepe in the trees, and build shelters from the raine. They feed upon fruit that they find in the woods, and upon nuts, for they eate no kind of flesh."

Battell (1613)

Science discovered the gorilla in 1847. Several plausible references to its existence appeared prior to that date, but these seem to have been dismissed as folklore. In the 5th century B.C. Hanno, a Carthaginian navigator, provided the earliest known description of apes, from the west coast of Africa (Reynolds, 1967; Yerkes & Yerkes, 1929), but judging from Hanno's description and location, he was referring to chimpanzees. The first reliable account of gorillas was that of Battell, an Englishman, published in 1613, in which he described the "Pongo" (gorilla) and the "Engeco" (chimpanzee) (quoted in Dixson, 1981; Hartmann, 1885; Reade, 1863; Yerkes & Yerkes, 1929). Another significant publication was Monboddo's Origin and Progress of Language (1774), in which an unnamed sea captain had heard of the "Impungu" from Angola, and compared it with the chimpanzee (quoted in Reade, 1863; Reynolds, 1967; Yerkes & Yerkes, 1929). In 1819, in Mission from Cape Coast Castle to Ashantee, Bowdich talked of the "Ingena" from Gabon (quoted in Dixson, 1981; Reade, 1863; Reynolds, 1967). These accounts apparently failed to arouse scientific interest (Yerkes & Yerkes, 1929).

Until the mid 19th century gorillas were known only from a few anecdotes. In the opinion of Yerkes and Yerkes (1929), Buffon delayed the scientific description of gorillas by decades by misnaming the apes: in his 20-volume natural history (1749-1766) Buffon considered that the information available to classify the apes was unreliable, so he hesitated to call them separate species, lumping them together instead (Reynolds, 1967). Many travellers, adventurers, and hunters must have been acquainted with gorillas, but they seem to have been confused with chimpanzees until 1847, when Savage and Wyman published the first scientific description of Troglodytes gorilla from Gabon. A missionary and an anatomist respectively, Savage and Wyman recognised the importance of a gorilla skull which came into their possession, having previously collaborated on a description of the chimpanzee. The authors adopted the name "gorilla" from Hanno and they believed that this was the ape described by Battell 200 years earlier.

The first specimens to reach Europe arrived from Gabon in 1851 and several important

works on the anatomy of gorillas were published shortly afterwards (see Hartmann, 1885; Yerkes & Yerkes, 1929). Interest in the gorilla was immediate, but increased greatly with the publication of The Origin of Species (Darwin, 1859), and Memoir on the Gorilla in which Owen (1865) stated that in its structure the gorilla was closest to man (Dixson, 1981). Unfortunately for the gorilla, numerous expeditions were mounted to collect specimens for museums, universities, and zoos (Reynolds, 1967). Garner (1896:199) spoke of the "reckless slaughter of them by the natives in order to secure them for white men", and the 728 gorilla skulls found in British collections (Groves & Napier, 1966) are testimony to the exploitation to which this ape has been subjected.

Scanty details of the gorilla's natural history were provided by Savage and Wyman (1847), and in the works of travellers and explorers (e.g. Reade, 1863), but much of this second-hand information was elaborated and incorrect. Du Chaillu wrote a sensationalised account of gorilla hunting, Explorations in West Africa (1861), which was later discredited (see Gray, 1861; Yerkes & Yerkes, 1929). I shall not review all of the works which relate stories of the gorilla's habits as the literature is extensive, and the little information it contains is generally inaccurate. Yerkes and Yerkes observed that "For the hundreds of gorillas which have been taken alive and kept for a few weeks...science has little indeed to show. The hundreds of specimens which have been shot by hunter-collectors...have yielded much to morphology, and the museums of the world are well stocked...it appears that the wastage of gorilla life and failure to utilize opportunities for study of mode of life and behavior are conspicuous, characteristic, and inexcusable" (1929:406).

From here on I shall cite chiefly publications describing the behaviour and ecology of western gorillas, as studies of mountain gorillas (which were discovered much later, in 1902) were reviewed in detail by Schaller (1963). However, two quotes from Schaller are pertinent here: "The literature on free-living gorillas is embarrassingly voluminous, considering the paucity of accurate information which it contains". It is often unclear whether "the information presented is based on direct observation, on verbal accounts by others, on intuition, or on mere paraphrasing of older writings, thus creating a highly inbred literature giving the appearance of truth through mere repetition" (1963:19).

B. EARLY STUDIES OF WESTERN GORILLAS

One of the earliest attempts to study gorillas in their natural environment was made by sitting in a cage and waiting for the gorillas to approach (Garner, 1896). Despite waiting for 112 days, Garner only glimpsed gorillas. His book Gorillas and Chimpanzees contained some highly anthropomorphised stories of gorilla behaviour, while their ecology remained virtually unknown. During the first half of the 20th century most information came via hunters from unreliable sources (e.g. Allen, 1931; Aschemeier, 1921; Petit, 1920). Even naturalists and zoologists provided dubious information (e.g. Dyce Sharpe, 1927; Urbain, 1940), and unreliable accounts continued to appear until the 1950s (e.g. Derochette, 1941; Liz Ferreira et al, 1945). Valker (1931) purported to publish the first precise data on the western gorilla's diet, but inaccuracies in the other data he presented cast doubt on the reliability of his information: for example, he asserted that silverbacked individuals form a separate species, and that gorillas have a rutting season.

The period of "general scientific inquiry" for mountain gorillas started with Derscheid (1927), Bingham (1932) and Pitman (1935) among others (Schaller, 1963:12), but very few scientific studies of western gorillas had been instigated by this time. Some scant information about nests and foods of gorillas in Cameroon was published by Bates (1905); and useful notes were provided by Garner (described by the editor of his 1919 article as the "greatest living authority on the domestic habits of the apes") and Ischac (1938). The first factual record of gorillas' social organisation, diet, and nests was written by a "reliable naturalist" from Nigeria (Anon, 1934 - F.S. Collier, a former conservator of forests, according to March, 1957). Malbrant and Maclatchy compiled a few details of gorilla distribution, ranging, and foods in Faune de L'Equateur Africain Francais (1949), but the 1950s were really a turning point in the study of gorillas: data on the gorillas' local distribution, density, ranging, group size, nests, and foods were published by Blancou (1951, 1955), a game inspector in Gabon, Merfield (1954, 1956), a hunter from Cameroon, and March (1957), a conservator of forests in Nigeria. Intensive scientific studies are reviewed below, while some others are referred to in discussions of my data.

C. CURRENT TAXONOMY & DISTRIBUTION OF GORILLAS

The genus Gorilla was established by Geoffroy-Saint-Hilaire (1858-61, see Schaller, 1963; Yerkes & Yerkes, 1929). Its taxonomy became the subject of some debate, and careful anatomical and geographical considerations by Coolidge (1929), Vogel (1961, cited in Schaller, 1963:12), and Groves (1967, 1970a) resulted in the recognition of three subspecies. Details of the relatively slight anatomical differences found between each subspecies are given in Dixson (1981), Goodall and Groves (1977), Groves (1986), and Maple and Hoff (1982).

Estimates of the past and present distribution of gorillas were described in detail by Coolidge (1929), Groves (1971), Gartlan (1980), and Schaller (1963), among others. Gorillas occur in many small and scattered populations in two distinct regions of West and Central Africa, separated by about 1000 km (Figure 1.1). Recently information concerning their present discontinuous distribution was compiled by Vedder (1987), and I shall use her summary as a basis for the following outline, together with information from Goodall and Groves (1977), and The IUCN Red Data Book (1988).

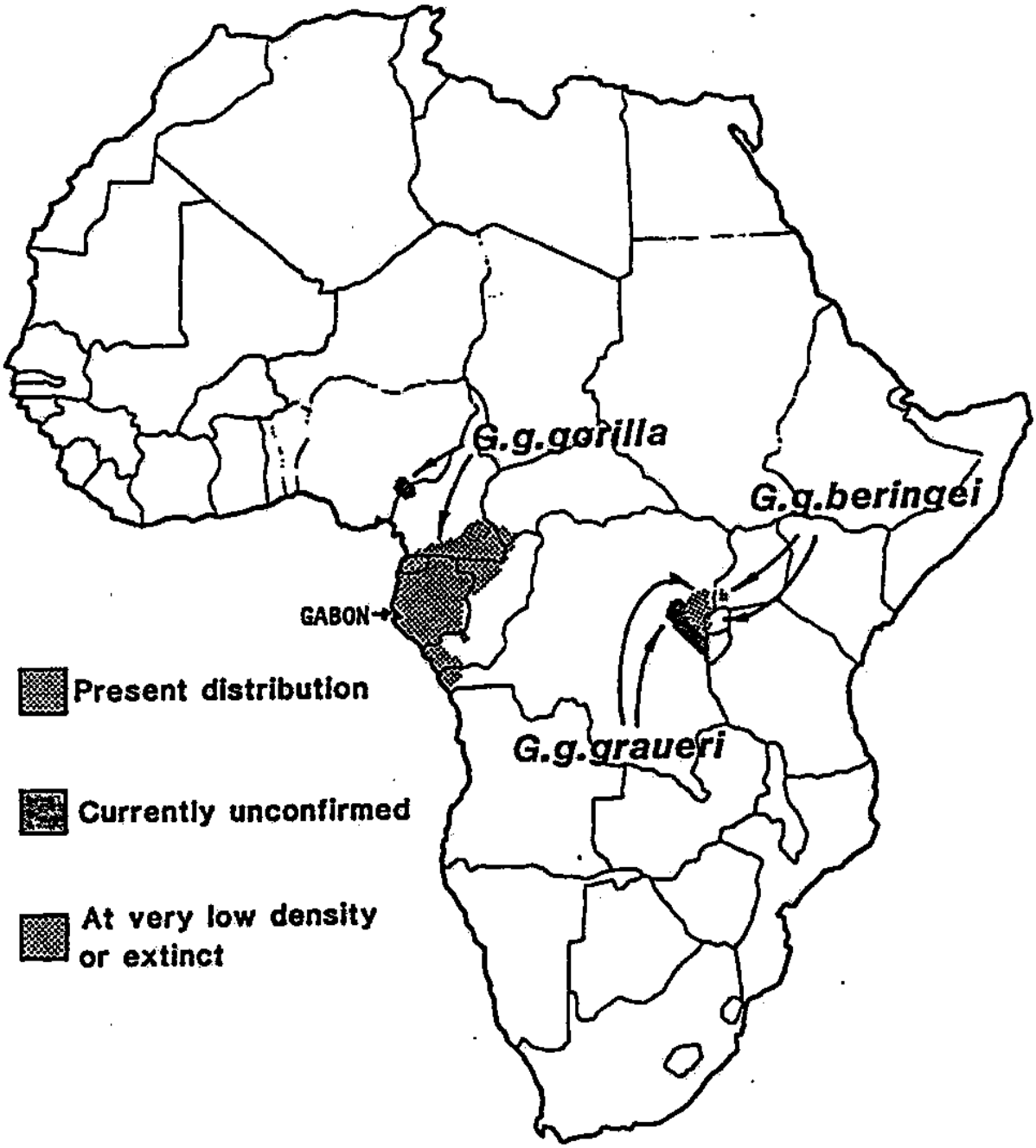
There are thought to be about 40,000 western lowland gorillas, Gorilla gorilla gorilla, remaining in the wild in seven countries. The distribution of this subspecies is centered around the forests of Gabon and Cameroon, extending into neighbouring Equatorial Guinea, Central African Republic (CAR) Congo, and Cabinda (an enclave of Angola). The persistence of an isolated population in Nigeria, close to the Cameroon border, has recently been reconfirmed (Harcourt et al. 1988), and large populations have been located in Gabon (Tutin & Fernandez, 1983a, 1984) and CAR (Carroll, 1986). The majority of western gorillas live at altitudes below 750 m, but in the western extreme of their range they are found at elevations up to 1500 m.

Gorilla gorilla graueri, the eastern lowland subspecies, last estimated to number 3000-5000 individuals, occurs only in Zaire: in tropical forests at about 600 m altitude, and in the Kahuzi-Biega region, 100 km south west of the Virungas, at between 2000 m and 2600 m. Although the population at Mt. Kahuzi inhabits highland areas, it is included under this subgrouping according to the currently accepted taxonomic classification (Groves and Stott, 1979).

Only about 400 mountain gorillas, Gorilla gorilla beringei, now remain. They are found in the Virunga Volcanoes region overlapping Zaire, Rwanda, and Uganda, ranging

Figure 1.1 Map Showing the Distribution of Gorilla Gorilla

(From Vedder/Nash, 1987)



between 2400 m and 4000 m, and in the Bwindi Forest (also known as the Impenetrable or Kayonza Forest) of South West Uganda.

The distribution of gorillas is apparently limited by the presence of forest. They are found not only in secondary vegetation, as previously implied (e.g. Gartlan, 1980), but in all types of forests, including mature and swamp forests (Tutin & Fernandez, 1984). Gorillas do, however, occur at lower densities in mature tropical forest than in regenerating vegetation (Emlen & Schaller, 1960; Tutin & Fernandez, 1984).

D. SCIENTIFIC STUDIES OF GORILLAS

Even before the end of the 19th century over 100 scientific reports of gorillas had appeared (see Keith, 1896), but these contained very little behavioural or ecological data. In 1951 Yerkes published a "plea" for gorillas to be studied, and asked "why the surprisingly slow progress of gorilla study during a century...when natural science has flourished exceedingly?" (1951:430). Western lowland gorillas have proved to be extremely difficult to study in the wild, due to the general inaccessibility of their habitats, their shyness, and the conditions in forests such as poor visibility. Tropical forests are probably the most complex ecosystems in which primates occur, and the data return per person-hour tends to be very low (Hladik & Chivers, 1978).

The two long-term studies of western gorillas took place in degraded habitats (i.e. areas which had been logged, or cleared for cultivation), and each had other limitations: the 18-month study of sympatric gorillas and chimpanzees in Equatorial Guinea by Jones and Sabater Pi (1971) resulted in less than 15 hours contact with apes, and much of their information was derived from second-hand sources. The precision of Sabater Pi's reporting has been questioned, as some of his published findings have been inconsistent (Goodall, 1974:136). During 15 months research in Cameroon, Calvert (1985) rarely saw gorillas; however, her work focused on nutritional analyses of food plants. The only other investigations of note also occurred in Cameroon: a survey of the Takamanda Reserve by Critchley (1968) lasted for 3.5 months, and a 2-month project by Butzler (1980) emphasised the impact of humans on gorilla populations, both direct (hunting for meat and crop-raiding) and indirect (the effects of forest exploitation).

Studies of eastern gorillas have virtually overshadowed anything that has been achieved with lowland gorillas. The neglect of the latter is perhaps due to the problems of

limited visibility in tropical forest (Figure 1.2), and of approaching gorillas, and may also be related to the highly endangered status of mountain gorillas. Ignoring popular accounts, surveys, and short-term studies (see Baldwin & Teleki, 1973), the landmark study of gorillas in their natural habitat was started by Schaller in 1959 at Kabara in Zaire. This was succeeded by Fossey's long-term research at the Karisoke field station, in Rwanda (see Fossey, 1983). A wealth of knowledge about the behaviour and ecology of mountain gorillas has been provided by the thorough investigations of Harcourt (e.g. 1978, 1979), Stewart (1977, 1984), Vedder (1984), and Watts (e.g. 1984, 1985), among others. Studies of the Bwindi population in Uganda have been undertaken recently (Butynski, 1985), while eastern lowland gorillas at Mt. Kahuzi, in Zaire have been studied by Goodall (1974, 1977), Casimir (1975, 1979), and Yamagiwa (1983).

The data from mountain gorillas are undeniably excellent, but problematic from two standpoints. Firstly, almost all information comes from a fraction of a small, isolated population at the highest end of the gorilla's altitudinal range (Harcourt et al, 1981). This subspecies is a relict population, inhabiting a refugium cut off by recession of the montane forest (Watts, 1983:25). The Virungas habitat is in itself extreme: it is unique and specialised (Goodall, 1974:7), being the coldest, marshiest, and most open area in which gorillas occur (Goodall & Groves, 1977). Yet mountain gorillas have been assumed to be representative of all gorillas. Secondly, even if the Virunga population were large (and mountain gorillas represent less than 1% of the world's population), montane forest is not the primary habitat of these apes if they evolved in lowland tropical forests, as seems likely (e.g. Cousins, 1982; Kortlandt, 1972; Tutin & Fernandez, 1984; Tuttle, 1975).

The paucity of existing data shows the need for research on the behaviour and ecology of lowland gorillas, especially if the prophesied rate of decline in the numbers of wild gorillas continues (Gartlan, 1980; Short, 1980; Yerkes, 1951). Gorillas are classified as vulnerable in the IUCN Red Data Book and listed in CITES Appendix 1 (Vedder, 1987). Lowland gorillas are threatened by loss or degradation of habitat, as logging and mining industries are established in previously inaccessible areas are 'opened up' (e.g. Gartlan, 1980; Tutin & Fernandez, 1987b). Gorillas are also killed for crop-raiding or for food in many areas, and a more recent trend has been their slaughter to supply meat for labour forces at forestry and mining camps (e.g. Butzler, 1980; Cousins, 1983; Harcourt & Stewart, 1980; Gartlan, 1980; Sabater Pi & Groves, 1972). Many were killed in drives to collect specimens for zoos and

research centres (e.g. Cousins, 1978; Sabater Pi, 1981), yet the population of gorillas in captivity may not be self-sustaining (Foose et al, 1986). Even though I shall not reiterate the arguments for conserving gorillas (see Dixson, 1981; Oates, 1986b), the need for intensive studies of the lowland subspecies is readily apparent.

E. STUDY-AREA

1. Background to the Study

In 1979 a symposium on the great apes of Africa was held at the inauguration of the Centre International de Recherches Medicale de Franceville (CIRMF) in Gabon (Short & Wier, 1980), at which Short remarked that "just as Gabon was the first country to bring the gorilla to the attention of Western science, so it is likely to be one of the last refuges of this magnificent animal in the wild". He also expressed the opinion that "Gabon's small human population, its economic wealth, and the enormous area of as yet undisturbed tropical forest make it the country of choice for a determined attempt to preserve the great apes in Africa, where they belong" (Short, 1980:11). Gabon has a large mineral wealth in its reserves of uranium, manganese, and oil, and the human population numbers 1.2 million, with an average density of only 4.6 people per km2 (Barret, 1983). Large areas of the interior are uninhabited as most towns and villages are located along roads and rivers (Tutin & Fernandez, 1984), and about 85% of the country is still covered by tropical forest, with savannas forming most of the remaining 15% (Caballe, 1978, 1983). Thus the prospects for the future of conservation in Gabon seem to be good.

CIRMF agreed to fund and support a nationwide census and survey of gorillas and chimpanzees in Gabon (Baulieu, 1980), the results of which indicated that the present population of gorillas numbers 35,000 ± 7000 (Tutin & Fernandez, 1983a). Thus Gabon is almost certainly the most important habitat country of the gorilla: the largest known extant population of gorillas occurs here in a vast area of intact forest. Chimpanzees are also found throughout most of the gorillas' range, providing an opportunity to study how these two closely related apes coexist.

Western Equatorial Africa is a significant area for primate conservation in global terms as at least 20 species of primates are found here (Oates, 1986a). Even before a new species of monkey, Cercopithecus solatus, was discovered in 1984 (Harrison, 1988), Chapman (1983) described the forests of Gabon as the area of greatest primate diversification in Africa.

This region is thought to have formed a forest refuge during the Pleistocene, and as such has a diverse and distinctive flora and fauna with a high level of endemism (see Oates et al, 1987). Gabon ranks among the top countries in the world with more than 10 million hectares of relatively undisturbed forest and a diverse primate fauna (Mittermeier & Oates, 1985), and was given a priority rating for the development of conservation and management programmes, due to its great species diversity, and large numbers of endemic and threatened species (Oates, 1986a).

2. The Lope Reserve

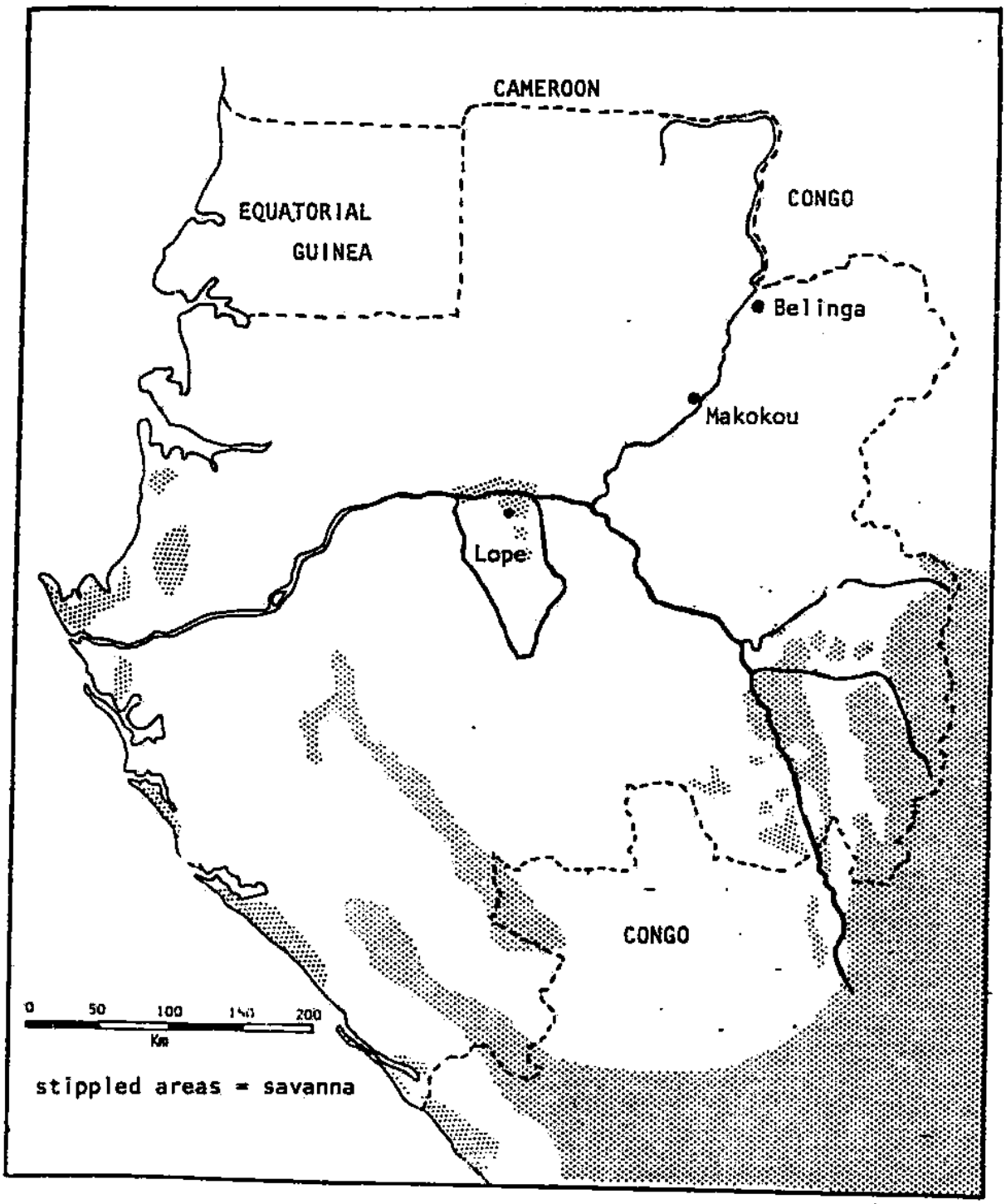
The Lope Reserve encompasses 5,000 km2 of mostly undisturbed tropical forest at 0o10'S, 11o 35' E (Figure 1.3). It straddles a plain between the Monts de Ndjole and the Francevillian basin, with altitudes ranging from 200 m to 500 m. Savannas and a network of gallery forests border parts of the Ogooue River, which forms the northern boundary of the reserve (Figure 1.4), parts of which were logged on a small scale between 1965 and 1979, to extract a single species of tree, Aucoumea klaineana. This area has been a game reserve since 1946, administered by the Ministere des Eaux et Forets, and is designated to become a National Park; it is the only large area of Gabon to benefit from legal protection (Tutin & Fernandez, 1987a). The Lope has been identified as a significant target area for conservation efforts (Oates et al, 1987), and was the subject of a recent survey by the IUCN (Nicoll & Langrand, 1986).

After conducting the census, Tutin and Fernandez established a research station, the Station d'Etudes des Gorilles et des Chimpanzes (SEGC), at the edge of the Lope forest in 1984. About 20 km2 of undulating forested hills form the study-area (Figure 1.5). The density of gorillas in the reserve as a whole was estimated to be 0.2 per km2 Tutin and Fernandez (1984), but is probably higher than this in the study-area. At least 14 species of primates occur at Lope, including chimpanzees, mandrills, and black colobus monkeys. These are listed in Appendix 1.1, along with all other mammals and some of the frugivorous birds sighted in the Reserve during the present study.

3. Climate

The central region of Gabon, including Lope, receives the least rainfall (IPN, 1983). Nearby Booue averages 1600 mm rainfall per annum (1951-1975), and during 12 months of

Figure 1.3 Map of Gabon Showing the Lope Reserve



the present study 1702 mm were recorded at Lope. The monthly distribution of rainfall is plotted in Figure 1.6, with long-term data from Booue for comparison. This region is characterised by 4 seasons: the major rainy season from October to mid-December, the short dry season from mid-December to mid-February, the minor rainy season from mid-February to May, and the long dry season from June to September. The amount of rain at Lope hardly differed from the annual average, but the pattern of distribution in 1984 was unusual. Rain was particularly heavy in May, but, more importantly, fell during July and August, in the long dry season. The consequences of this rainfall for the phenology of the forest will be discussed in Chapter 3. The long dry season is an exceptional phenomenon in equatorial regions (IPN, 1983), and the total rainfall received in central Gabon is much less than in some other equatorial regions of West Africa. Where similar low levels of rainfall are recorded in parts of Asia the forests are deciduous (Hladik, 1973). Persistent cloud cover during the long dry season in Gabon is thought to maintain the evergreen nature of the forest during this critical period, as it results in lower temperatures, and reduced evaporation, and humidity levels stay high. Thus the rate of water loss from the soil is minimised (Hladik, 1973). The mean relative humidity in the forest is over 80% for all months of the year (St. Aubin, 1963), and the diurnal variation is only 4-8% (IPN, 1983).

The annual mean maximum and minimum temperatures recorded at Lope were 21.7oC and 29.1oC respectively, and monthly values are given in Figure 1.7. It can be seen that minimum temperatures were almost constant, and that diurnal variation was greater than seasonal fluctuation. Figure 1.6 also shows that the long dry season was the coolest period of the year: the maximum mean temperatures during July, August, and September were less than 28oC, whereas temperatures increased to a maximum of 32oC at the beginning of the rainy seasons, in February and October, when bright sunshine and clear skies followed rain storms.

In comparison, the ambient temperatures for eastern gorilla populations are much lower than at Lope. At Kahuzi-Biega mean temperatures oscillate between 12.4oC and 24.6oC (Goodall, 1974), and are even lower in the Virunga Volcanoes: 3.8oC and 14.8oC (Watts, 1983), due to the high altitude. Above 3000 m temperatures drop below zero at night. The total annual rainfall (1823 mm) and the pattern of rainfall distribution in the Virungas are similar to at Lope, but at high altitude there is little sunlight, heavy cloud, frequent mists or fog, and the vegetation is sodden most of the time (Watts, 1983:30).

Figure 1.6 Monthly Distribution of Rainfall at Lope

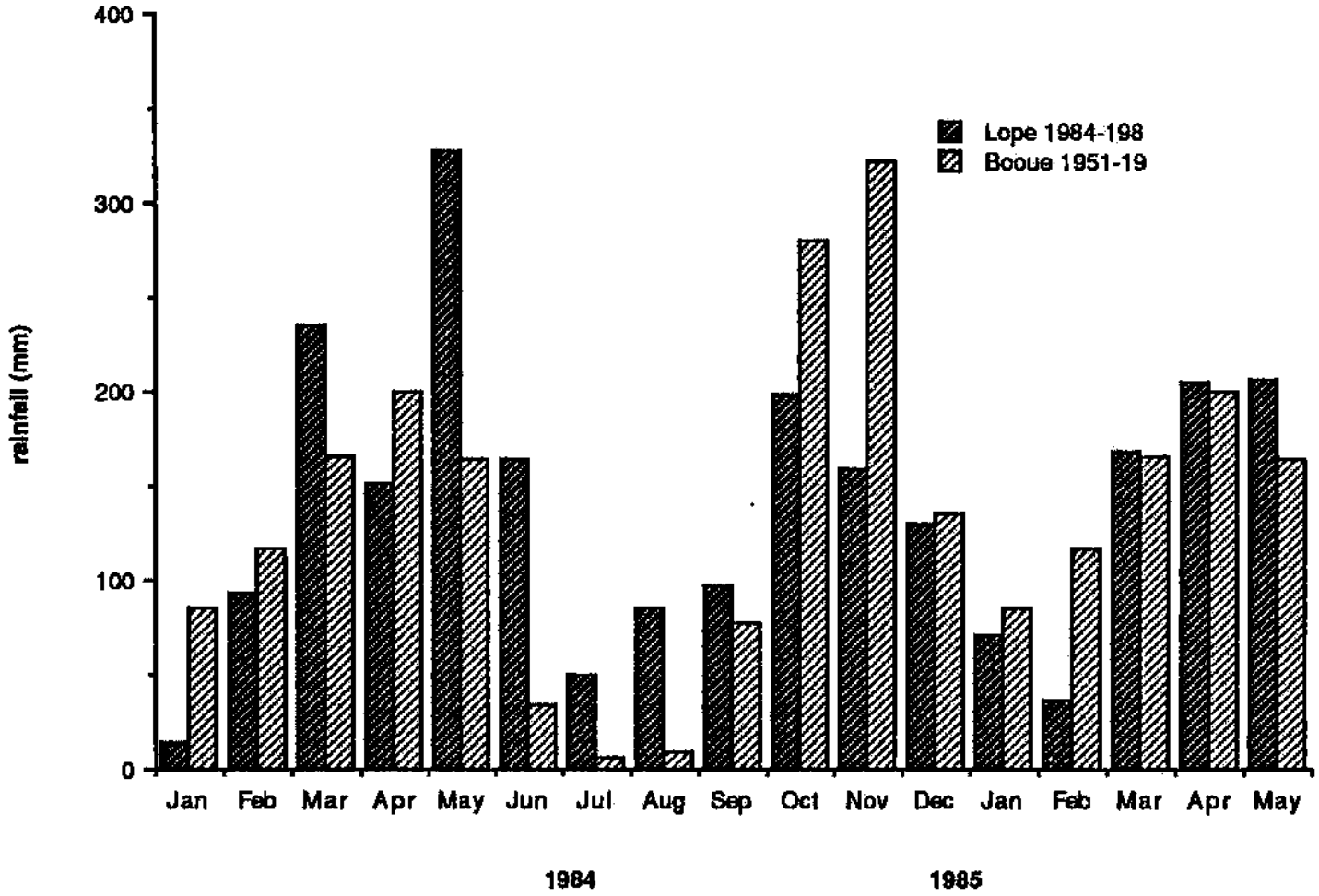
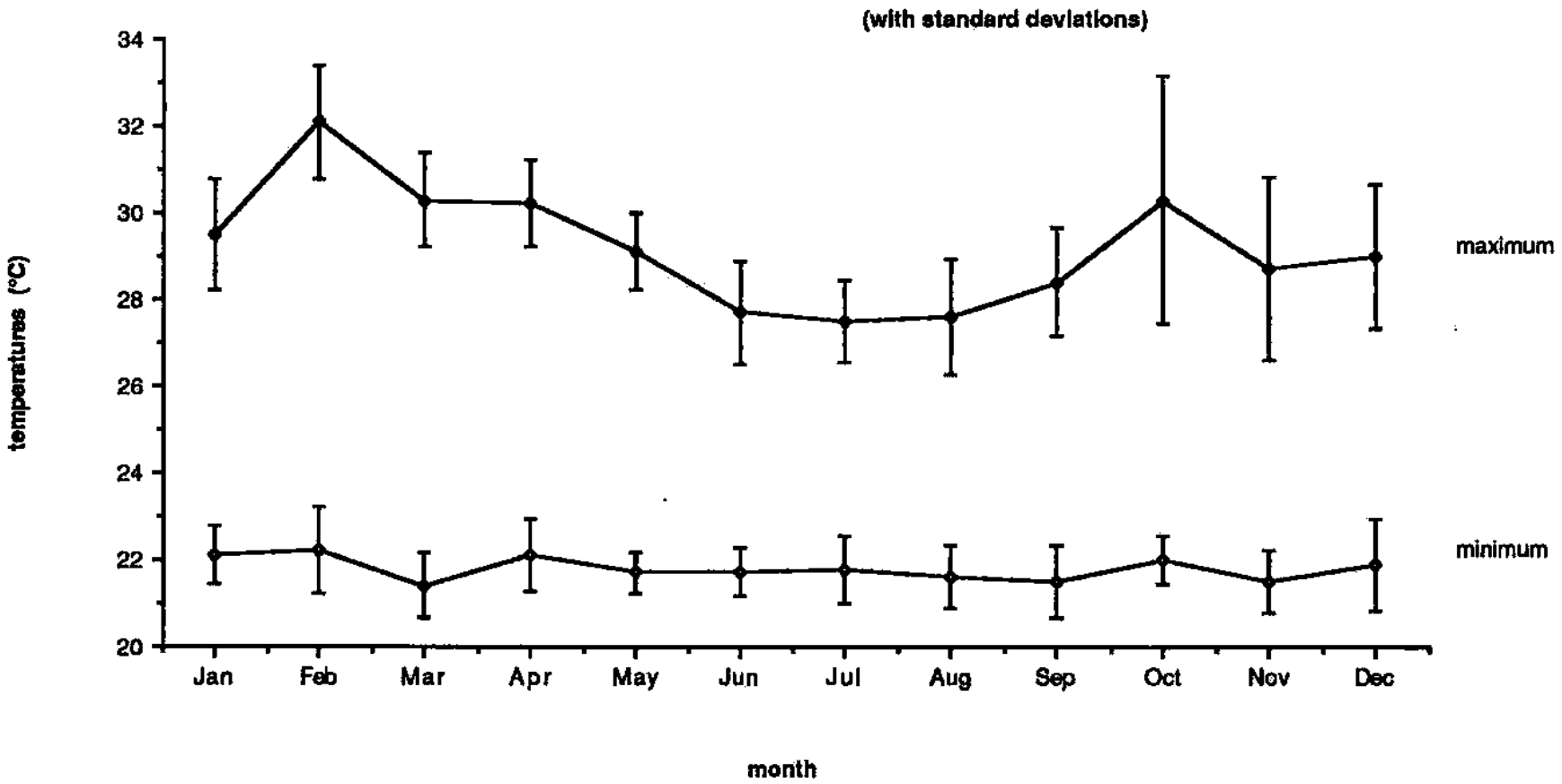


Figure 1.7 Mean Monthly Air Temperatures at Lope 1984



F. AIMS

The general aim of this study was to collect data on the behavioural ecology of gorillas during 16 months in the field, from January 1984 to May 1985, with the long-term aim of 'habituating' the apes to our presence. Exaggerated accounts in the early literature portrayed gorillas as exceedingly ferocious and dangerous, never running away from humans (e.g. Allen, 1931; Aschemeier, 1921; Derochette, 1941; Dyce Sharpe, 1927; Savage & Wyman, 1847). However, gorillas do not attack without provocation; for example, if they have been injured, or surprised at close range (Garner, 1896; Jenks, 1911; Petit, 1920; Reade, 1863). Persons who stand their ground and behave in a non-threatening manner are unlikely to be harmed (Merfield, 1954). Sabater Pi (1966) found that of seven attacks by gorillas in Equatorial Guinea during a 10-year period, six occurred as self-defence against hunters, or resulted from sudden surprise encounters.

Thorpe (1956, cited in Schaller, 1963:311) defined habituation as the relatively persistent waning of a response as a result of repeated stimulation which was not followed by any kind of reinforcement. Repeated neutral contacts with humans can lead to a reduction in the gorillas' fear, and eventually to the acceptance of an observer as a passive part of the environment, a process known as habituation. Wild gorillas were successfully habituated by Schaller, Deschryver, Fossey, and other workers at Karisoke field station. A similar level of acceptance was aspired to by researchers at Lope (Chapter 7).

Dietary niche is one of the fundamental parameters which constrains the behavioural ecology and evolution of a species, and so one of the first requirements of this ecological study was to describe the western gorilla's diet. Wrangham (1979) stated that all the apes should have basically similar dietary requirements, and the other species of great apes are all described as frugivores (e.g. Ghiglieri, 1987). Gorillas, however, have been classified as folivores (e.g. Bouliere, 1985; Clutton-Brock & Harvey, 1980; Eisenberg et al, 1979; Richard, 1985:165), a generalisation based on our knowledge of mountain gorillas, even though there have been suggestions that the western subspecies is more frugivorous since the earliest reports about their habits: Savage and Wyman (1847) recounted that gorillas fed on similar fruits to those eaten by chimpanzees; Jenks (1911) related that gorillas ate many fruits from forest trees and shrubs; Petit (1920) and Valker (1931) also mentioned that gorillas ate a fruit diet; Yerkes and Yerkes (1929:539) described the lowland form as "more largely frugivorous"; and Owen (1865, cited in Maunder 1885:772) stated that the gorilla's anatomy

accorded with statements concerning its frugivory. Also, Blancou (1955) commented that in Cameroon the gorilla's diet varied in quality according to season, which I suggest was most likely due to a fruit component in the diet.

I have already expressed doubts about the accuracy of some of these early reports, but more substantial evidence has been accumulated (e.g. Sabater Pi, 1966, 1977), and a strong indication of frugivory came from a study conducted in north-east Gabon, which concluded that lowland gorillas can no longer accurately be classed as folivores (Tutin & Fernandez, 1985).

The extent of frugivory in western lowland gorillas may have a profound influence on other aspects of their ecology: for instance, food-searching may be oriented towards seeking out irregularly dispersed fruiting trees; gorillas may come into direct and intense competition with a large number of sympatric frugivores; use of the habitat may differ substantially from that observed in eastern gorilla populations; and ultimately there may be differences in demography and social structure. Tropical forests differ from montane forests in several ways which may have important consequences for gorillas; for example, they are more diverse and as a result resources are less predictably distributed in time and space (e.g. Milton, 1981b).

Throughout this thesis comparisons are drawn with other populations of gorillas. However, as few data are available for eastern lowland subspecies, there is a strong emphasis on the mountain gorillas from the Virunga Volcanoes, and the western lowland gorillas at Lope.

In summary, the principal aims of this study were:

(i) to describe and to characterise features of the habitat, and to quantify the distribution and availability of the gorillas' foods (Chapter 3);

(ii) to investigate feeding ecology by identifying the components of the gorillas' diet, by estimating the extent of seasonal variation in food selection, and by evaluating potential competition for these resources (Chapter 4);

(iii) to investigate the gorillas' use of their habitat, including nest-building (Chapter 5), and to define the home ranges of individual groups (Chapter 6).

CHAPTER 2: METHODS

A. INTRODUCTION

The ultimate goal of the SEGC is the habituation, without provisioning, of gorillas and chimpanzees to permit a detailed comparative study of their behavioural ecology. All methods of field research were chosen with habituation in mind. Frequent contacts with the same individuals are necessary to achieve habituation, so the daily objective was to locate a 'known' gorilla group. Trackers were not employed as local people considered gorillas to be aggressive and dangerous, thus their reactions to apes would not have been compatible with habituation. Observers should behave calmly and attempt to reassure the gorillas by mimicking grooming or feeding, preferably from a seated position, whilst imitating 'belch' or 'contentment' vocalisations. Similar methods caused least disturbance to the mountain gorillas habituated by Schaller (1963), and Fossey (1972, 1983). The eastern lowland gorillas habituated by Deschryver were studied by Goodall (1974), Casimir (1975), Yamigawa (1983), and Mori (1983).

Previous attempts to 'bait' gorillas with bananas, sweet potatoes, maize cobs, and sugar cane have failed (e.g. Baumgartel, 1958). Provisioning the gorillas at Lope with artificial supplies of food was rejected as a method of accelerating habituation, as some natural behaviour patterns in chimpanzees have been modified by provisioning (e.g. Wrangham, 1974; Reynolds, 1975).

Essential equipment included a compass, binoculars (I used Leitz 10 x 40), and a pair of secateurs, to cut through dense tangles of ground-level vegetation with minimum noise. Schaller (1963:23) advocated wearing the same drab-coloured clothing each day, and we wore wellington boots and thick cotton, full-length, army-surplus shirts and trousers, which afforded protection from sharp-edged plants, and biting insects. 'Nalgene' water-proof note books, simple hand-drawn line maps, and small polythene bags for collecting samples were carried. Later in the study Motorola HT90 'walkie-talkies' were acquired, which enabled contact between observers, and better co-ordination of movements, and thus improved the efficiency of searching.

Systematic searches of the study-area were carried out between 05.30 hr and 18.00 hr, generally from 07.30 hr to 15.00 hr. Searching was often carried out by pairs of

researchers, primarily as a safety precaution. However, working as a team was useful when tracking, as 2 observers could confirm the direction from which chestbeats or vocalisations were heard, follow trails in parallel lines, and observe a greater number of individuals during contacts. When possible we worked singly, to maximise the area covered during any one day. The decision to search a given area was based on the results of the previous day's work, or on our knowledge of the location of fruiting trees which might attract gorillas.

Field-notes included standard information on the routes taken and areas searched, researchers present, time spent in the field, weather conditions, all mammal sightings, and the distribution and reproductive status of some fruit sources. Detailed notes, written in longhand, included descriptions of the gorillas' vocalisations, reactions to observers, methods of food processing, and of individuals to aid future recognition of group members. After all contacts the gorillas' movements were mapped and summary sheets completed. Close attention was paid to the feeding activities of monkeys, and fruit-eating birds, such as hornbills, to help locate fruiting trees.

Remains were attributed to gorillas by direct means (i.e. sight, sound, or smell) or indirect evidence (e.g. knuckle- and foot-prints; association with nests or faeces). All observation sites, nest-sites and trails were carefully investigated; food-items and faecal samples were collected, and detailed notes taken. Locations were determined using duplicated maps and by recognition of familiar features. The maps, on a scale of 10 cm:1 km, were drawn initially from aerial photographs, then old forestry roads, major animal-paths, and streams were plotted using a 'Topofil Hipchain' to measure distance and compass. As we became familiar with a network of animal-paths we could move rapidly between areas, and were more successful at keeping up with the gorillas. There were several advantages to using a system of paths already in existence: it was not necessary to invest time and effort making or maintaining trails; the habitat was not altered or damaged, and we did not create new trails which may have influenced the travel-patterns of large mammals.

The ease with which the gorillas' trails could be followed varied in relation to the density of food traces, and the time they had spent at any one location, for instance travelling groups did not leave any food-remains. We learned to recognise and age

feeding signs; freshness was affected by the rate of drying out, which was determined by the climate, although Aframomum remnants tended to look older if they had been rained on. We usually had to predict the gorillas' routes, as trails were rarely continuous. If a trail was lost we moved forward in parallel directions to pick it up again.

A contact was defined as the researcher being within auditory range of one or more gorillas whose approximate whereabouts were known. An observation was defined as having at least one gorilla in view. During contacts we tried to sit in an open position, so that the gorillas could see us, as they tended to be less alarmed when the position of a potential threat could be localised (cf. Schaller, 1963:22). Photography and direct eye-contact were avoided, and binoculars were used sparingly unless the distance between the subjects and observer was greater than 50 m. Observation from a concealed position was valuable for data collection, but contributed nothing to habituation. Short-term gains (collection of data) were sometimes sacrificed for the long-term aims of the project (habituation), as gorillas often fled once they became aware of our presence. If gorillas were contacted at close range (<10 m), or in vulnerable situations, such as feeding in trees, we remained hidden to avoid panicking them. Such close encounters could easily occur during heavy rain, when subtle sounds were masked, and tracking was often abandoned in such conditions. Fossey (1972) stated that pursuing a group hindered habituation, but as it was difficult to maintain contact with gorillas in tropical forest we usually attempted to follow from a distance. A flexible strategy was adopted, so that groups were not followed if they were frightened, or if the silverback was excited and displayed with increasing intensity.

Throughout the study we collected opportunistic data on the diets of other mammal and bird species, particularly those using the same food sources as the apes, notably the forest elephant, monkeys, and frugivorous birds, such as hornbills and touracos.

Not every field-day was devoted to tracking apes. Other activities included bi-monthly censusing of all primates along a predetermined 4 km circuit, botanical transects, and collecting data on phenology (phenology is the study of organisms as they are affected by climate). Assessing the vegetation is important, as as the quality of the habitat influences a species' demography and behaviour (e.g. Dunbar, 1987), and detailed 'background' information contributes to the coherance of our understanding of

ecological systems (Leigh, 1982).

Most of the data presented here were collected by myself and Dr. Caroline Tutin, but the field-notes of other researchers working at SEGC during this study have been made available to me.

B. PARTICULAR METHODS IN DETAIL

1. Climatological Data

Rainfall was collected in a rain-gauge at camp and measured daily at 07.00 hr. A resetable maximum and minimum thermometer was used to record daily temperatures. Opportunistic humidity readings were taken throughout the day, using a standard wet and dry bulb thermometer. The thermometers were nailed to a tree in the forest, 1 m above ground, in a well-ventilated and shady position.

2. Vegetation Analysis

Several methods of sampling were used to describe the habitat and assess food availability with a view to understanding the gorillas' ranging patterns and habitat use. Some earlier studies of gorillas employed a method which was suitable for the quantification of herbaceous vegetation (Calvert, 1985; Vedder, 1984; Watts, 1984), but not for larger scale sampling of trees, as at Lope. I chose transects as a relatively speedy method of collecting data on the forest structure and composition.

a) Transects.

i) Trees. Strip-sampling was used to estimate the density and distribution of trees. A 1 km line was cut on a compass bearing, traversing an area of forest between two old logging tracks. All trees with a dbh (diameter at breast height measured 1.3 m above ground) greater than 10 cm, and found growing within 5 m of the line were enumerated and labelled with aluminium forestry tags. For inclusion in the sample the centre of the trunk had to fall within the 10 m strip. The dbh of each trunk was recorded, above any buttresses or aerial roots, and multiple trunks were measured individually. Those trunks which split above 2 m were measured at the point of division. A 10 cm cut-off encompassed most trees of the mid-storey and all of the upper canopy, whilst excluding

shrubs and saplings, which are less important for describing forest composition. Each tree-species was identified, or leaf, flower and fruit samples were collected.

A further 3 km were assessed to sample ridge tops, valley bottoms, slopes and stream banks, including a circuit used for phenological monitoring and to census primates. These areas were accessible from existing paths, so it was not necessary to cut new transect lines, thus enabling a greater total area to be sampled (4 ha).

Densities of trees were calculated from dbhs to give an indication of species diversity, and relative biomasses were calculated from basal area, which is correlated with tree-height and crown-volume (e.g. Oates et al. 1980). The dominant species recorded were used to characterise the vegetation and for comparisons with other areas of tropical forest.

ii) Marantaceae & Zingiberaceae. These large ground herbs were a major source of food and nesting material for gorillas at Lope (cf. Jones & Sabater Pi, 1971; Tutin & Fernandez, 1985), so precise estimates of herb densities were made. Individual stems were counted along a 1 km transect using a strip width of 1 m. A further 2 km with a strip width of 10 m was surveyed by recording the presence or absence of herbs. The mean wet weight of edible parts per stem was calculated, and hence the biomass of potential food per unit area (see Rogers & Williamson, 1987).

b) Phenology.

i) Trees. Fruit and, to a lesser extent, the leaves of trees were important components of the gorillas' diet at Lope (cf. Tutin & Fernandez, 1985), so fruit and leaf production were quantified every month to investigate seasonal variation in food availability. Labelled individual trees were examined using binoculars. A 5-point linear scale was used to score the proportions of tree canopies composed of new, mature and old leaves, or the potential crop, in the case of fruits and flowers. The advantages of this system were:

(i) it was easily repeated;

(ii) it gave an estimate of relative crop size;

(iii) it indicated variation in production and species availability between months;

(iv) it allowed direct comparison of trees of different species and sizes.

Ripeness of fruits was not described systematically, as not all species showed obvious signs of ripening, such as colour changes. Major changes in reproductive status

which were observed between monthly samples were added to field-notes. By the end of the study 344 individuals of 83 species were monitored, including several non-foods which formed major components of the habitat. Up to 10 individuals per species were sampled, but only one individual of some rare species was located. Individual trees of species that were rare, but important as a source of food for gorillas and which were not found on the transects, were mapped so that they could be monitored when in fruit.

ii) Marantaceae & Zingiberaceae. Megaphyrinium and Haumania were abundant and important food-species for gorillas, so new leaf-production by these two genera of Marantaceae was quantified during a bimonthly census along a 1 km transect. Ten plants of each type were chosen at random in each 100 m stretch, and all new and mature leaves were counted, from which the relative proportion of new leaves was calculated.

Production of new growth by Zingibers was not monitored systematically, as there appeared to be little variation in the amount of food they provided, other than the seasonal production of fruit. Flower and fruit production by both families was noted during the census. Other herb species were not selected as they were found to be insignificant sources of food for gorillas.

c) Identification of Plants.

Samples of all plants eaten by gorillas or used for nest-building, and of all tree species found on the transects, were collected. Leaves and flowers were pressed and stored in airtight containers; fruits were sectioned and dried, pressed, or preserved in 10% ethanol. Identifications were made at Kew Gardens, and at the Museum of Natural History in Paris.

3. Nests

Standard checksheets were completed for all nests, with maps of site locations. Nest size, type of construction, and distribution were recorded. Strict guidelines were adopted to distinguish between the nests of gorillas and chimpanzees:

(i) nests on the ground or on fallen tree trunks were attributed to gorillas;

(ii) nests in trees closely associated with and judged to be the same age as nests on the ground were attributed to gorillas;

(iii) nests above a height of 2 m in trees and not associated with ground nests were

attributed to chimpanzees.

There is little overlap in the heights at which the two species of apes nest, and at least one gorilla always builds its nest on the ground (Schaller, 1963:181; Tutin & Fernandez, 1983a).

Nests were classified into 8 types (cf. Tutin & Fernandez, 1983a):

(i) NO CONSTRUCTION: gorilla slept on bare ground, sleeping site recognised by impression in soil and presence of fresh faeces;

(ii) MINIMAL CONSTRUCTION: a few stems of herbaceous plants bent to form a rudimentary pad;

(iii) HERBACEOUS: many stems of herbaceous plants bent to form a mattress with a roughly circular depression;

(iv) MIXED HERBACEOUS & WOODY: similar to (iii) but woody lianas, shrubs, or detached branches were also incorporated into nest;

(v) DETACHED WOODY: nest constructed exclusively from woody branches broken from shrubs or trees;

(vi) ATTACHED WOODY: similar to (v), but branches still attached to shrub or tree;

(vii) CAVE: gorilla slept on bare earth, beneath a 'roof' of vines;

(viii) TREE: nest located above ground in a tree or shrub, formed by breaking and bending woody vegetation into a sleeping platform.

Nests were also classified by age (cf. Tutin & Fernandez, 1983a):

(i) FRESH: vegetation was green and not wilted;

(ii) RECENT: vegetation was dry and changing colour;

(iii) OLD: vegetation was dead, but nest was still intact;

(iv) ROTTING: nest was beginning to disintegrate.

4. Analysis of Faeces

During previous studies of primates, the proportion of the diet composed of various food categories has been estimated as (i) a percentage of the stomach contents of dead animals (e.g. Gautier-Hion, 1980); (ii) the frequency with which foods were chosen (e.g. Strusaker, 1975); (iii) the time spent feeding on each item (e.g. Fossey & Harcourt, 1977); or (iv) by visual assessment of the amount of food ingested converted to fresh weight (e.g.

Hladik, 1977). At Lope observation was limited, and the bulk of data on foods were derived from faecal analysis. This method is particularly important in determining whether some food-types which may not be observed at all, such as insects, are ingested. A combination of direct observation and faecal analysis is an ideal way of obtaining information on feeding (Moreno-Black, 1978), and these were the methods used, with additional information collected on trails.

All fresh faeces were collected, unless damaged by dung beetles (Scarabeidae), termites, or rain. They were sealed in polythene bags and weighed with a spring balance. Age-sex classes were estimated from the diameter of the dung, (cf. Schaller, 1963:90):

(i) SILVERBACK: > 7.3 cm

(ii) ADULT: 5.5-7.2 cm

(iii) JUVENILE: 4.0-5.4 cm

(iv) INFANT: < 2.5 cm

Samples were washed in 1 mm wire-mesh sieves to remove the dung matrix. The particulate contents were examined and all recognisable items were quantified and recorded. Seeds and other items occurring in small numbers were counted, whilst items occurring in large numbers (>100), or which were not found in discrete quantities (e.g. stem-fibre, green-leaf fragments) were rated as rare, few, common, or abundant. Samples of each food-item were collected and preserved for identification; seeds were dried, and insect remains placed in 10% ethanol. Several criteria were used to differentiate the faeces of gorillas from those of chimpanzees:

(i) POST-OBSERVATION: collected after seeing gorillas;

(ii) POST-AUDITION: collected after hearing gorillas;

(iii) found in association with gorillas' NESTS;

(iv) found on TRAILS left by gorillas.

These guidelines, together with differences in the dung odour and consistency, were usually sufficient to classify specimens. If doubt remained samples were examined under a microscope and the presence of Troglodytella gorillae, a large intestinal ciliate, was used to verify that the faeces were of gorilla origin (Garin et al, 1982).

5. Statistics

Data-sets were coded into numerals and transcribed onto character punching sheets, in a format compatible with computer facilities at the University of Stirling. Analyses were carried out using SPSSx (Statistical Package for the Social Sciences, version x). Unless otherwise stated Analysis of Variance (ANOVA) and 2-tailed Pearson correlations were used, all tests were 2-tailed, and 0.01 levels of significance are given.

CHAPTER 3: VEGETATION

"Nor indeed do I recommend African forest life to anyone. Unless you are interested in it and fall under its charm...it is like being shut up in a library whose books you cannot read, all the while tormented, terrified and bored. But if you do fall under its spell it takes all the colour out of other kinds of living" adapted from Mary Kingsley (1897:102)

A. INTRODUCTION

Systematic quantitative habitat analysis is a prerequisite to understanding the ecology of gorillas in lowland tropical forest. In this chapter the floristics and physiognomy of the forest at Lope are described, providing a basis for long-term study. My aims are:

(i) to describe the temporal and spatial availability of plant species which provide food for gorillas;

(ii) to define vegetation types within the study-area and thus enable investigation of the gorillas' differential use of their habitat;

(iii) to provide a general description for comparison with other areas of tropical forest and other habitats where gorillas have been studied.

A simple distinction between 'primary' and secondary forest is often made, and gorillas' habitats have been categorised in these superficial terms (e.g. Sabater Pi, 1977). Secondary vegetation is the plant community which regenerates when forest is disrupted, for example, by logging or agriculture. Initial colonisation by precocial 'pioneer' species causes subtle changes in the intensity of light reaching ground level, and impedes wind movements. These modifications to the environment allow other species with different requirements to invade. Young secondary forest is recognisable by its low, broken canopy, dense tangles of herbs and vines at ground level, and few large trees. Light-loving (heliophilic) pioneer species are present in large numbers, monospecific stands are common, and plant diversity is low (Swaine & Hall, 1983; Brokaw, 1985a).

The classical view of succession (i.e. changes which take place in the structure and composition of regenerating forest) is that ultimately a stable or 'climax' forest is established. The implication that mature forests are in equilibrium is now disputed (e.g. Connell, 1978). Studies of 'gap dynamics' have demonstrated that secondary colonization on a small scale is continuous, even within mature forest, following disturbance by animals and tree falls (e.g. Hartshorn, 1978; Whitmore, 1978). 'Climax' forest is an abstract state which will not be attained, although changes in structure and composition occur at slower rates as forests mature (Whitmore, 1984). Richards (1952:381) stated that "old secondary forest is difficult or impossible to distinguish from undisturbed, virgin forest". Species compositions are overlapping, but densities change, as there is a slow increase in the proportion of 'primary' species, thus the scale between secondary and mature vegetation is a continuum (Bazzaz & Pickett, 1980). I shall use the term 'mature' forest to avoid some of the preconceptions elicited by 'primary', which are that such forest typically has a high (30-40 m) continuous canopy and sparse ground vegetation (e.g. Andrews & Aiello, 1984).

The forests of Gabon have been studied in detail and over 3000 plant species catalogued (e.g. Aubreville, 1967; Hladik & Halle, 1973; Caballe & Fontes, 1978). Much of this work has centred around M'passa in the north-east, and relatively little is known about Lope. The Lope is an area of evergreen lowland tropical forest, part of the Congo-Guineen equatorial forest block (Aubreville, 1968; Caballe & Fontes, 1978). Selective logging took place in the late 1960s, with the removal of 1-2 stems/ha of Aucoumea klaineana, a species of tree endemic to Gabon. There are marshy areas but no swamps, and aerial roots, buttresses, palms and epiphytes are not common. The density of lianas is low, perhaps less than 5% total forest leaf biomass (Harrison, 1984).

I shall make comparisons with other sites in Gabon, other areas of tropical forest where chimpanzees or gorillas occur, and other regions where gorillas have been studied. Gorillas in West Africa have been studied most in areas of predominantly secondary forest (Jones & Sabater Pi, 1971; Calvert, 1985), while eastern gorillas are best known from montane areas. Chimpanzees are found at Kibale, in Uganda, a moist evergreen forest at higher altitude than Lope, but with a similar annual rainfall. Kibale

has some characteristics of both lowland rain forest and montane forest (Strusaker, 1975; Oates, 1977; Waser, 1977). This area has also been selectively logged and has an abundant understorey. Data are also available from Budongo forest, also in Uganda (Eggeling, 1947) where chimpanzees were studied by Reynolds and Reynolds (1965). And of the 3 main sites where bonobos have been studied in Zaire (Yalosidi, Wamba and Lomako), the most comprehensive vegetation data are available from Lomako (Badrian & Malenky, 1984).

In this chapter I shall assess the structure of the forest, the density and diversity of tree species present, and the phenology of primary production to estimate spatial and seasonal variation in the amount of food available to gorillas. I shall also consider the effects of gorillas on their habitat, and some of the other important influences on the vegetation at Lope.

B. FOREST STRUCTURE & COMPOSITION

1. Physiognomy

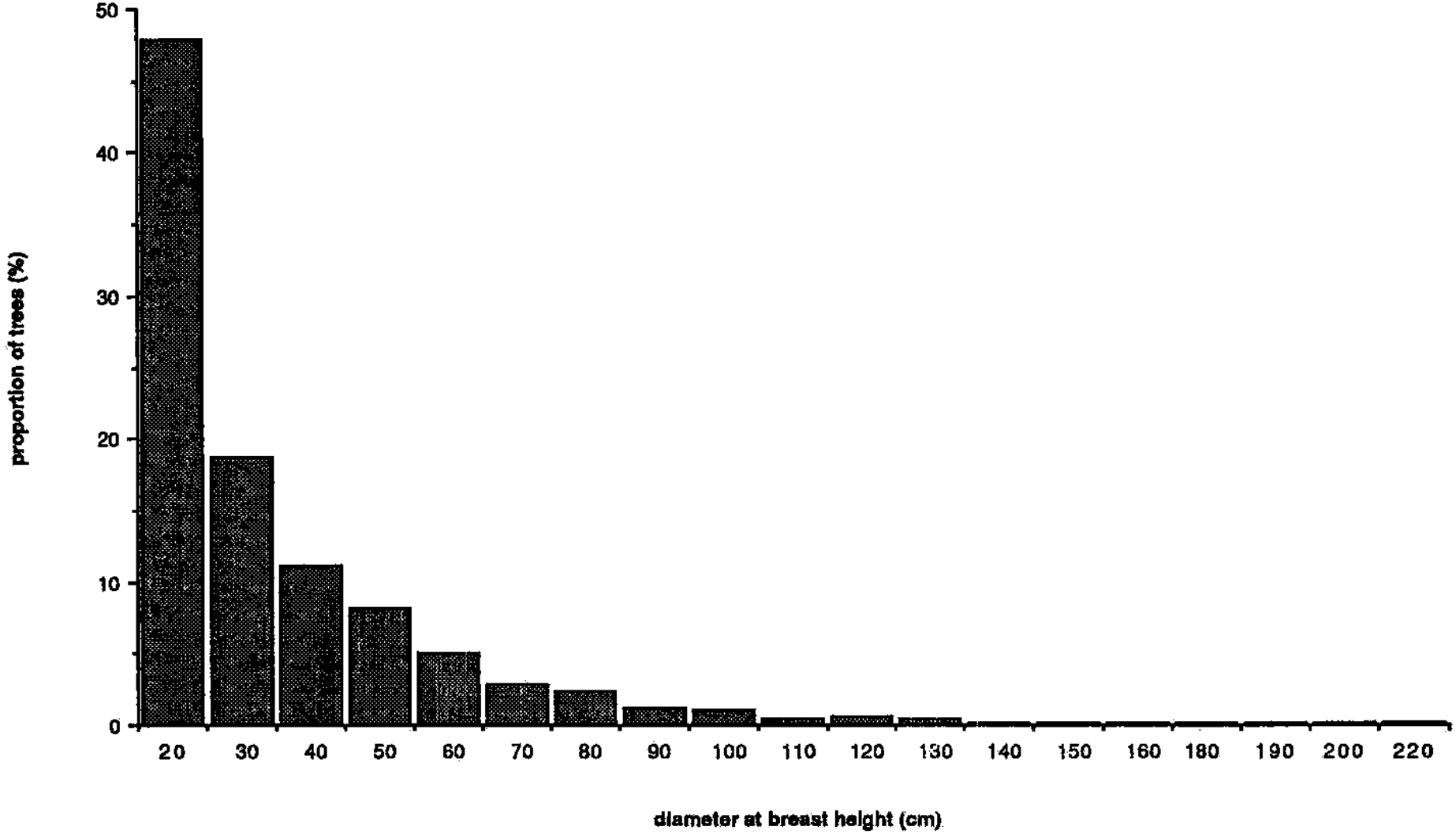
The descriptors of forest structure analysed were: the heights of trees; classes of trunk diameters; basal area of trees; and the density and distribution of herbaceous vegetation.

a) Heights of Trees.

The heights of 191 trees along 400 m of transect ranged from 5 m to 40 m. The distribution of tree heights was negatively skewed, with 62.4% in the 10-20 m class. This sample included all trees with a dbh (diametre at breast height) greater than 10 cm. The Lope forest had no obvious layers, but a fairly uneven canopy, with occasional emergent trees up to 40 m tall. The concept of horizontal stratification in tropical rain forest has been refuted (e.g. Hladik, 1978; Richards, 1983; Alexandre, 1984), as such divisions are subjective, and assume that disturbances in mature forest are rare (Halle, Oldeman & Tomlinson, 1978:333).

b) DBH. Over 50% of trees measured less than 20 cm dbh (Figure 3.1); 35 trees per hectare were 'big' (i.e. >60 cm dbh, cf. Webb et al, 1967), which was at least equivalent to

Figure 3.1 Structure of Forest at Lope by DBH



some other areas, such as M'passa which averaged 22 per hectare. The proportion of trees in each size-class is an indicator of forest maturity (e.g. Knight, 1985). Once sampling thresholds were standardised, the population structures at the present study-site, at M'passa, and at another site in the Lope reserve (Harrison, 1984) were judged to be similar.

c) Basal Area. Basal area or 'stocking' is a estimate of biomass calculated from dbh measures, assuming circular cross-sections of trunks. The pan-tropical mean basal area of trees is 33 m^2/ha (Dawkins, 1958, 1959, cited in Brunig 83). Basal area at Lope (40m^2/ha, >10 cm dbh) was comparable to other sites in Gabon (Table 3.1).

d) Terrestrial Herbaceous Vegetation (THV). Mature forest is usually described as relatively open at ground level with a denser understorey in light gaps (e.g. Richards, 1952:5). However at Lope Aframomum and Marantaceae were common throughout the study-area (7.7 stems/m^2, Rogers & Williamson, 1987). Haumania often formed thickets and 'vine towers', and several species of Marantochloa grew in streams and in marshes in the bottoms of valleys. No quantitative comparative data are available from other forest sites; the only other known study of THV density lumped all herb species together to measure relative obstruction by the undergrowth (Dubost, 1979). The high density of THV at Lope may be an important structural component of the forest for gorillas.

2. Spatial Distribution of Trees

Several detailed studies have shown that tropical trees are unevenly distributed in space and that many species are highly clumped (e.g. Hubbell & Foster, 1983). According to Kershaw and Looney (1985:155) causes of patterning are always present, but difficult to identify and quantify. Variance:mean ratios have been used to demonstrate irregular spacing (e.g. Strusaker, 1975; Milton, 1980:30; Watts, 1983:83). However, such measures assume random sampling and should not be used for transect data, which is composed of contiguous quadrats (D.M. Newbery,pers.comm.). Complex analyses of pattern were not performed on the data from Lope as a threshold level of 20 individuals per species was required (D.M. Newbery, pers.comm.), which was met by only 5 of the 138

Table 3.1 Tree Biomass in Tropical Forest in Gabon

STUDY SITE		THRESHOLD DBH	BASAL AREA (m2/ha)
Lope, Gabon	(present study)	10 cm	40.7
" "	" "	16 cm	39.1
" "	(Harrison, 1984)	16 cm	37.5
M'passa, Gabon	(Hladik, 1984)	5 cm	35.0
" "	" "	30 cm	26.7

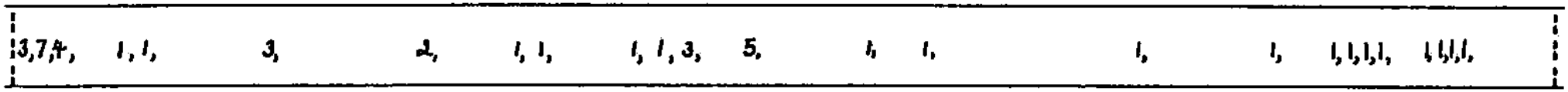
Table 3.2 Dominant Families of Trees in Forest at Lope

FAMILY	SPECIES PRESENT (total = 138)	% INDIVIDUAL TREES (N = 1538)	% BASAL AREA (10 cm dbh)
Sterculiaceae	2	25.8	11.5
Ebenaceae	7	12.9	5.5
Caesalpiniaceae *	13	8.9	13.6
Annonaceae	7	8.5	1.8
Mimosaceae *	8	7.1	10.7
Burseraceae	5	4.4	17.2
Papilionaceae *	2	1.4	7.7

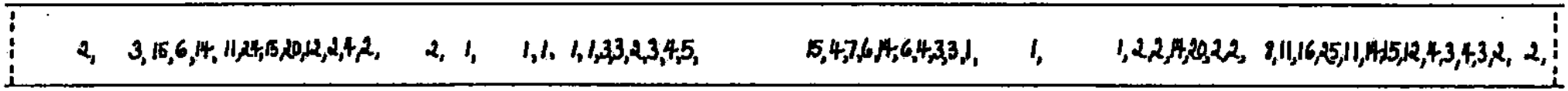
* these 3 families are all Leguminosae, which together account for 17.4% of the population, and 32.0% of the basal area.

Figure 3.2 Distribution of Some Common Tree Species Along 4 km of Transects at Lope

Aucoumea klaineana N = 45

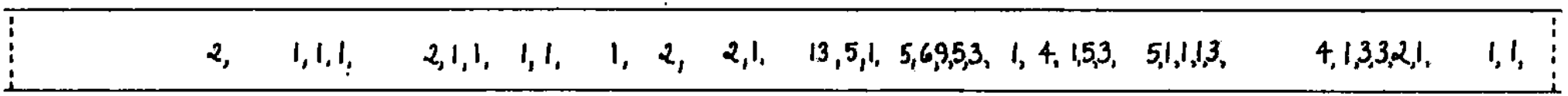


Cola lizae N = 384



Dialium sp. N = 18

Diospyros dendo N = 105



Diospyros polystemon N = 84

Numbers represent individuals counted per 50m x 10 m block.

species in the sample. However, some species' distributions are effectively illustrated by Figure 3.2, which shows their patchy or 'contagious' distribution.

3. Vegetation Types

Forest types are sometimes classified by one or more species with limited distribution, and the Lope falls within an area grossly defined as 'foret a Aucoumea' (Caballe, 1983). The dominant families in Gabon as a whole are the Caesalpiniaceae, Mimosaceae and Myristacaceae (Aubreville, 1968). At Lope the Burseraceae and Caesalpiniaceae dominated the forest, while the Mimosaceae and Myristacaceae were less common (Table 3.2).

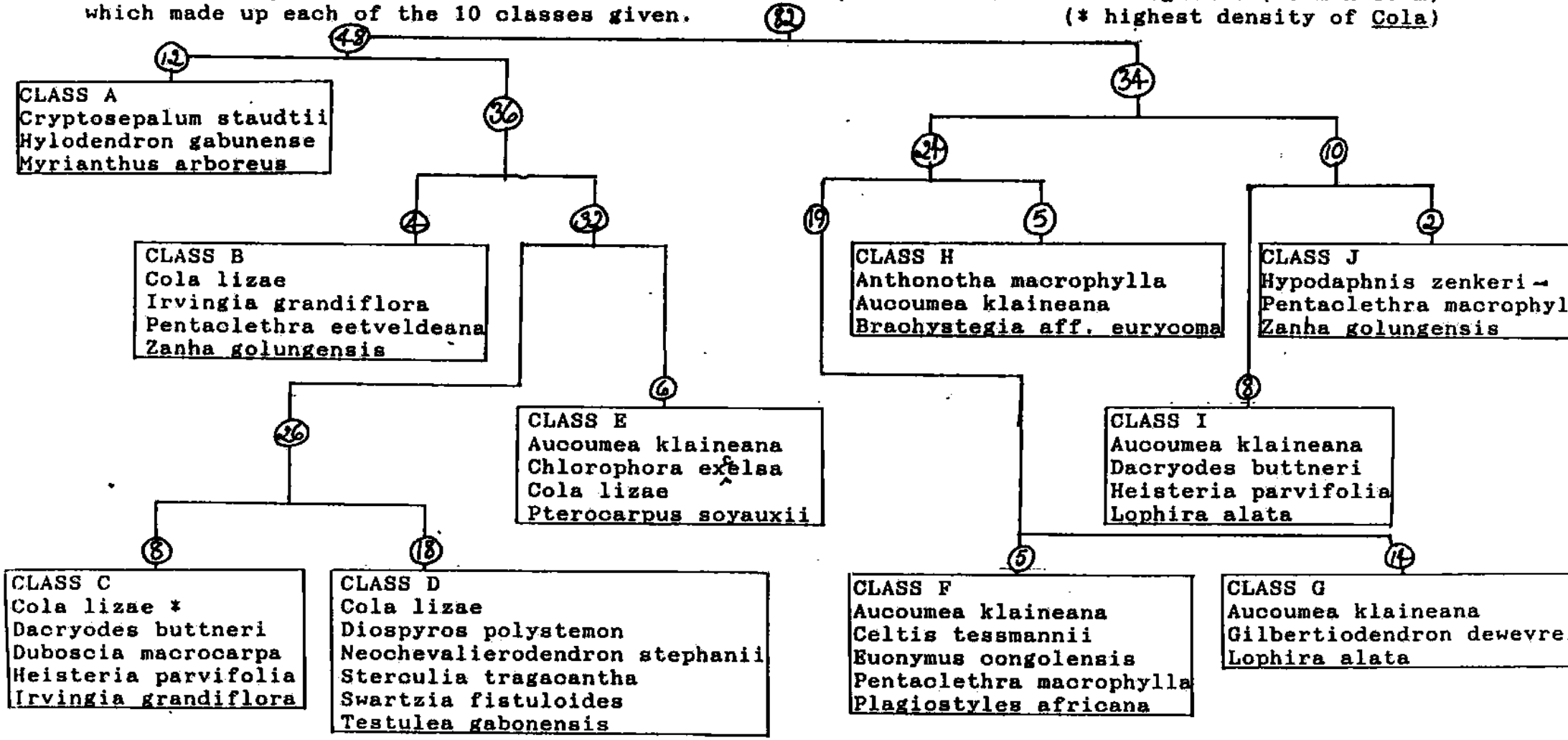
Vegetatation types were difficult to distinguish by simple visual assessments. A Two-Way Indicator Species Analysis (TWINSPAN, Hill, 1979) was performed on the transect data to distinguish forest types by species composition and density. This program classifies species according to their ecological 'preferences', forming a divisive heirachy from all sections of the transects (set at 50 m). The 'primary ordination', a crude initial dichotomy, separated Cola lizae from Aucoumea klaineana and Lophira alata. These species occurred together, but were more likely to be found in separate samples. Further divisions, known as the 'refined ordination' and the 'indicator ordination', were taken to differing levels; they were terminated once the distinctions made would no longer be recognisable in the field (N = 4). A threshold of more than 3 individuals excluded rare species, to prevent random correlations. This treatment produced 10 classes of forest, illustrated in Figure 3.3. 'Indicator' species were identified according to their 'fidelity' to a particular class. The output from this analysis, an ordered 2-way phytosociological table of species and transect segments, is given in Appendix 3.1. Retrospective classification of the areas used by gorillas was not possible, but the ordination indicated the abundance of each vegetation type, and provided a basis for future data collection.

4. Diversity & Density of Trees

Tropical forests are characteristically heterogeneous and the central basin is richer

Figure 3.3 TWINSPAN Classification of the Forest at Lope

"Indicator" species classified from 4 ha of transects, with the number of segments (50 m x 10 m) which made up each of the 10 classes given. (* highest density of Cola)



in species than other regions of Africa (Richards, 1952:257). In 4 ha of transects at Lope 1538 trees of 138 species representing at least 32 families were recorded. Appendix 3.2 lists the 94 species (68.1%) identified (89.9% of individuals).

The number of tree species per hectare ranges from 20 to 223 in tropical forest (Whitmore et al, 1985). At 35 sp/ha, Lope seems to have a species richness similar to Kibale (36 sp/ha, Struhsaker, 1975) and Budongo (39 sp/ha, Eggeling, 1947) in Uganda. However, such comparisons are problematic, as there is a non-linear relationship between number of species recorded and the area sampled (Richards, 1952:249).

Many species (N = 54, 39.1%) occurred only once on the transects, but one species of tree, Cola lizae, formed a quarter of the sample. This masked the large number of rare species which were present, and may have reduced the apparent diversity. The Shannon-Weaver index of diversity (Pielou, 1966) was calculated to be 3.34 using the formula:

$H = - \Sigma\ pi\ \log_{10} pi$ where Σ = sum of, and pi = sampling probability.

Another simple indicator of diversity is the number of species which formed 50% of the population. No standard criteria have been adopted for this measure, and results have depended on whether species' frequencies or basal areas were selected. Table 3.3 presents values for Lope together with data from some other sites. Although it can be seen that the forest at Lope was as diverse as the other West African sites, and that the montane habitat of eastern lowlands gorilla is less diverse, this table also illustrates the difficulties of trying to make comparisons.

The apparent disparity between measures can be reconciled by taking into account the size and distribution of individual trees using 'Importance Values' (IVs). IVs have been used both by plant ecologists (see Kershaw & Looney, 1985) and primatologists (e.g. Badrian & Malenky, 1984; Rumiz et al, 1986). IVs are derived from the addition of relative frequency, relative density and relative dominance of each species and some values for Lope are listed in Table 3.4.

Data from Harrison (1984) show that even within the reserve there were notable differences in forest composition. For example, only 7 of the 'top 10' species were common to both sites, and 4 of the predominant species in the present study-area were not

Table 3.3 Diversity Measures of Tree Species in African Forests

STUDY SITE		THRESHOLD	NUMBER OF SPECIES
1. 50% Individuals in Population			
Gabon	(present study)	10 cm dbh	6
"	" "	16 cm dbh	7
"	(Harrison, 1984)	16 cm dbh	9
Uganda	(Waser, 1977)	10 m height	5
Uganda	(Struhsaker, 1975)	10 m height	4
Zaire	(Casimir, 1975)	none	2
2. 50% Biomass			
Gabon	(present study)	10 cm dbh	8
"	" "	16 cm dbh	8
"	(Harrison, 1984)	16 cm dbh	7
3. Proportion of Population Formed by 10 Most Common Species			
a) Individuals:			
Gabon	(present study)	10 cm dbh	60.9%
"	" "	16 cm dbh	58.1%
Uganda	(Strusaker, 1975)	10m height	79.4%
b) Biomass:			
Gabon	(present study)	10 cm dbh	54.8%
"	" "	16 cm dbh	55.5%
"	(Harrison, 1984)	16 cm dbh	58.2%

Table 3.4 "Top 20" Tree Species at Lope

SPECIES	IMPORTANCE VALUE
Cola lizae	43.6
Aucoumea klaineana	24.1
Pterocarpus soyauxii	17.7
Diospyros polystemon	11.0
Pentaclethra macrophylla	10.7
Trichilia prieureana	10.4
Lophira alata	9.5
Pentaclethra eetveldeana	8.6
Xylopia sp.	7.6
Berlinea bracteosa	7.0
Anthonotha macrophylla	6.8
Diospyros dendo	6.5
Cryptosepalum staudtii	6.4
Hylodendron gabunense	5.5
Irvingia grandifolia	5.3
Heisteria parvifolia	5.1
Distemonanthus benthamianus	4.4
Dacryodes buttneri	4.2
Duboscia macrocarpa	4.0
Swartzia fistuloides	3.3

IMPORTANCE VALUE = sum of (Rf + Rdo + Rde)
where:
f = frequency (N. plots in which species recorded)
Rf = relative frequency (f/total freq. of all species x 100)
do = dominance (total basal area)
Rdo = relative dominance (do/total dominance x 100)
de = density (total number of trees sampled)
Rde = relative density (de/total dens. of all species x 100)

recorded at Harrison's site. To evaluate the degree of similarity in species composition between the Lope and some other areas where apes occur I devised a Species Overlap Index (SOI) (Table 3.5). There were several biases in the sampling: published lists were selective, usually food-species; the proportions of unidentified species were not given; differing criteria were chosen for inclusion in the analysis, such as height or trunk diameter; and plot sizes were not standardized. Despite these drawbacks, the rank order of SOIs demonstrated the degree of similarity between habitats. On the whole, floristic overlap decreased as distance increased, as expected.

5. Discussion & Conclusions

There are few similarities between the forest at Lope and the habitat of mountain gorillas, which live on volcanic peaks between about 2400 m and 4000 m. Much of the vegetation is open woodland with a dense herbaceous layer standing up to 2.5 m high (Schaller, 1963:52), and the slopes most often used by the gorillas are covered with thick low foliage and nearly devoid of trees (Fossey, 1974). The volcanic peaks of the Virunga volcanoes are often bathed in mist, favouring the development of moss, which stunts the growth of other vegetative forms. Forest height decreases with augmenting altitude and increasing humidity, creating easily defined strata (Leigh, 1975). The abundance of epiphytes also increases with altitude and a concurrent decrease in the density of trees. The trees have a different morphology from those in tropical forest, reaching only 10-12m in height.

Most studies in the Virungas have quoted qualitative observations and botanical surveys to describe the vegetation. Fossey (1976) sampled 3 plots each of 10 m^2, but these were not reported in subsequent publications. Goodall (1974) also cited botanical surveys when describing the montane forest at Kahuzi-Biega in Zaire. Casimir (1975) sampled the forest at Mt Kahuzi by drawing biotope maps from aerial photos and measuring species' frequencies on transects.

Few direct comparisons can be made between the Lope and the habitats of eastern gorillas, except that the vegetation in the eastern regions was less diverse, and tree densities were lower than at Lope. There was no floristic overlap between the Virungas

Table 3.5 Species Overlap Index

STUDY SITE		NUMBER OF SPECIES	SOURCE	S.O.I. *
Gabon				
Lope	(Harrison, 1984)	86	p	65.1%
Gabon	(Caballe, 1978)	77	p	45.5%
M'passa	(Gautier-Hion et al, 1985b)	83	f	42.2%
"	(Hladik, 1982)	44	p	39.8%
"	(Dubost, 1984)	73	f	38.4%
Other African Countries				
Eq.Guinea	(Jones & Sabater Pi, 1971)	34	p	38.2%
Cameroon	(Hoshino, 1985)	50	f	36.0%
Zaire	(Kano & Mulavwa, 1984)	48	f	35.4%
Zaire	(Badrian & Malenky, 1984)	60	f	29.2%
Cameroon	(Calvert, 1985)	31	f	23.1%
Cameroon	(Gartlan et al, 1978)	114	p	19.3%
Uganda	(Reynolds & Reynolds, 1965)	35	f	15.7%
Uganda	(Strusaker, 1975)	51	p	8.8%
Uganda	(Waser, 1977)	57	p	7.9%
Tanzania	(Wrangham, 1975)	149	f	6.7%
Zaire	(Casimir, 1975)	23	p	4.3%

Key: p = plant species list
f = food " "

* Calculation of SOI values
sum (N. species also at Lope) + (N. genera also at Lope x 0.5) converted to % of species composing list.

and lowland tropical forest.

The studies of Jones and Sabater Pi (1971) and Calvert (1985), in Equatorial Guinea and Cameroon respectively, concentrated on gorillas feeding in logged areas and fields, which were degraded habitats. Jones and Sabater Pi (1971) simply used Forest Service surveys to show "abundance" (frequency) of some "common" species.

The richness of the forest at Lope, indictated by the number of species recorded per hectare, was equivalent to that recorded in other areas of Gabon and in Uganda. The floristic overlap between several areas of central Africa demonstrated a degree of similarity, and the population structures of 3 sites in Gabon were also shown to be similar. The biomass of trees at Lope was a little above the pan-tropical mean, but comparable to other sites in Gabon. Tree distribution was characteristic of diverse tropical forests, in that species were irregularly spaced, and some were clumped.

C. PHENOLOGY

Trees illustrate the phenological activity of a forest community, and fruits are an important food source for most mammals in tropical forest (Emmons et al, 1983). Flower, fruit and leaf production was monitored in 346 trees of 83 species, as was new-leaf production by Marantaceae.

1. Phenology of Trees

a) Introduction.

Various problems have 'cropped up' with descriptions of plant production: some authors have represented the activity of communities by the proportion of *INDIVIDUAL* plants (e.g. Raemaekers et al, 1980; Davies, 1984); others have chosen plant *SPECIES* (e.g. Croat, 1975; Milton et al, 1982); only a few have incorporated a measure of *INTENSITY* (e.g. Alexandre, 1980; Wheelright, 1985), such as the 0-4 scores used in the present study. I gave equal weight to tree species, rather than individual trees, because species' sample-sizes ranged from 1-10, and were not constant throughout the study. Also, some rare but important food-species were chosen, creating a selective bias in the sample. Scores for intensity are presented as median values, as the majority of trees

were inactive and thus scored zero. The high values for August and September resulted from differences in sample sizes, and perhaps these early data should be ignored. When sampling began in August 174 trees of 69 species were monitored; in October the size of the sample increased to over 200 trees; by January 1985 it had reached 300.

b) Leaf Renewal.

Median scores for new, mature, and senescing leaves of all tree species are illustrated in Figure 3.4. Three leafing patterns were described by Hladik (1978) and similar trends were observed at Lope:

(i) evergreen trees never renewed more than a quarter of their canopies at once;

(ii) deciduous species shed all their leaves at once and were then covered with thin, limp leaves for a few days;

(iii) other species lost their leaves in peaks with flushes of new leaves, but were not deciduous.

Patterns of leaf production were not ascertained for 40 species during the sampling period, however 24 were found to be evergreen, and 19 were deciduous. At Lope the proportion of mature leaves was always greater than 77% of the canopy of the entire community. Senescence was fairly constant (ignoring idiosyncratic August) with a small peak in November. Deciduous activity was observed in 12 species, but known for an additional 7 from Harrison (1984). These red, pink, pale yellow, or pale green flushing trees provided abundant localised food-sources for primates, including gorillas.

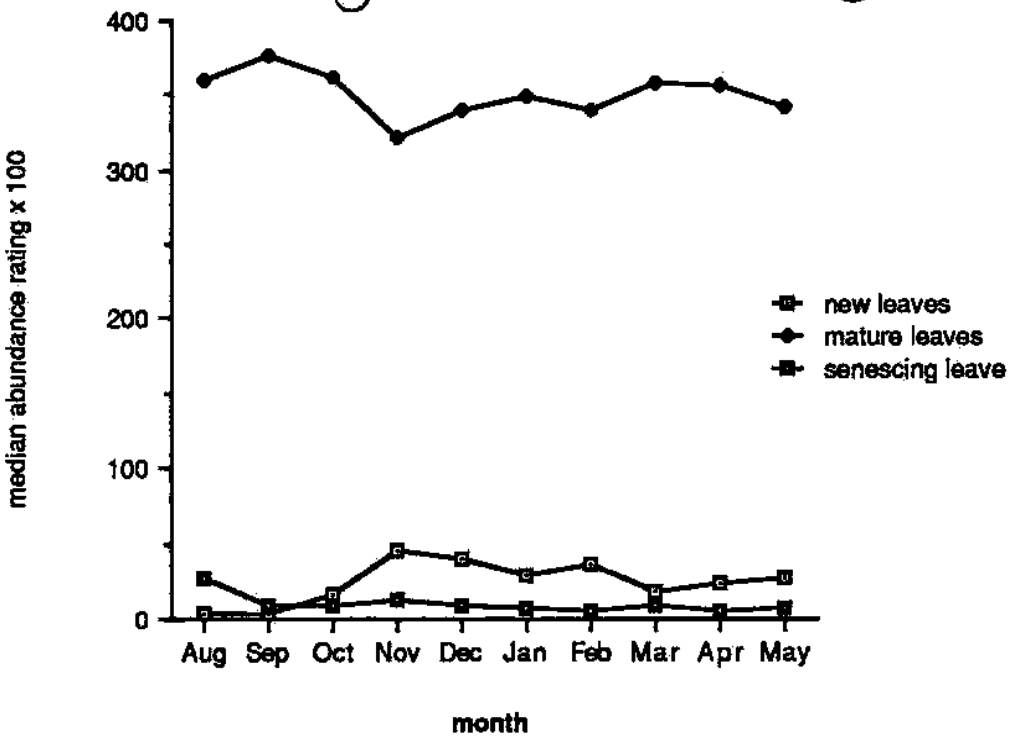
Figure 3.4 shows 2 peaks in new-leaf production, which coincided with the what would have been the onset of the 'normal' rains in November and February (the usual timing of the rains, as deduced from the long-term data, see Chapter 1). Production of new leaves correlated with the long-term rainfall data for the preceeding month ($r=.8519$, $p=.002$), although this relationship was not significant for the amount of rain which actually fell at Lope ($r=.6161$, $p=.058$). Synchronicity of leaf renewal was observed in 12 species: the deciduous ones.

c) Flowering.

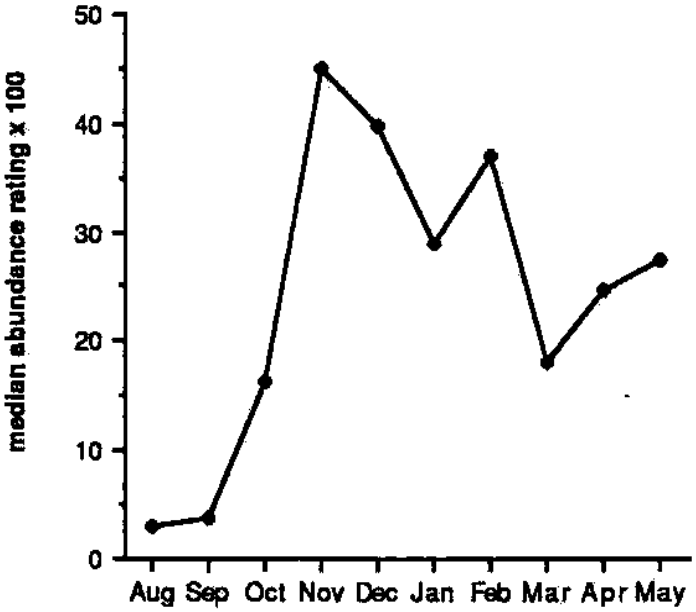
Three patterns of flowering in tropical forest in Ghana were identified by

Figure 3.4 a) Leaf Renewal by Trees at Lope

abundance ratings: 0 = no leaves; 4 = 100% canopy cover



b) new-leaf production only



Lieberman (1982):

(i) almost continous flowering, simultaneous with fruiting;

(ii) alternate flowering and fruiting throughout the year;

(iii) relatively short periods of seasonal activity.

At Lope flowering peaked in November, and in February when the dry season was prolonged (Figure 3.5). The proportion of species bearing flowers in any one month ranged from 2.7% to 22.8%, but 39 species (47.0%) were never seen to flower. Upperstorey (>15 m) and understorey (<15 m) trees were analysed separately. Because rain fell during the long dry season, the activity of upperstorey trees was suppressed in November. A burst of activity in February followed an unusually dry January, but this was restricted to the upperstorey trees. Understorey species seemed to be less sensitive to unusual fluctuations in the pattern of rainfall. In fact a significant correlation was found between the long-term rainfall data and flowering of understorey trees the following month ($r=.8985$, $p<.001$), although no relationship with rainfall was demonstrated for trees of the upperstorey, or the community as a whole. This fits with Croat's (1975) observation that the tall upperstorey is more exposed, and likely to show a quicker response to climatic triggers. The anomolies presented by August and September have been explained above.

In some species the duration of flowering was brief (less than 2 weeks), in others it was extended (more than 2 weeks), but no precise information was available as data were collected on a monthly basis. Some species were highly co-ordinated and flowered intensely for a few days, and were therefore missed by monthly sampling (e.g. Pentaclethra macrophylla in April 1985). Of the 44 species which flowered, 29.5% (13) seemed to be synchronous.

d) Fruit Production.

The proportion of species which bore fruit in any one month ranged from 20.3% to 34.1%; 33 species (39.8%) did not fruit during the study. These may have been male trees of dioecious species, which do not bear fruit after flowering. These species produce unisexual flowers which are found on separate individuals, and include most of the Burseraceae, Ebenaceae and Euphorbiaceae. The proportion of dioecious species at Lope

Figure 3.5 Flowering of Trees at Lope

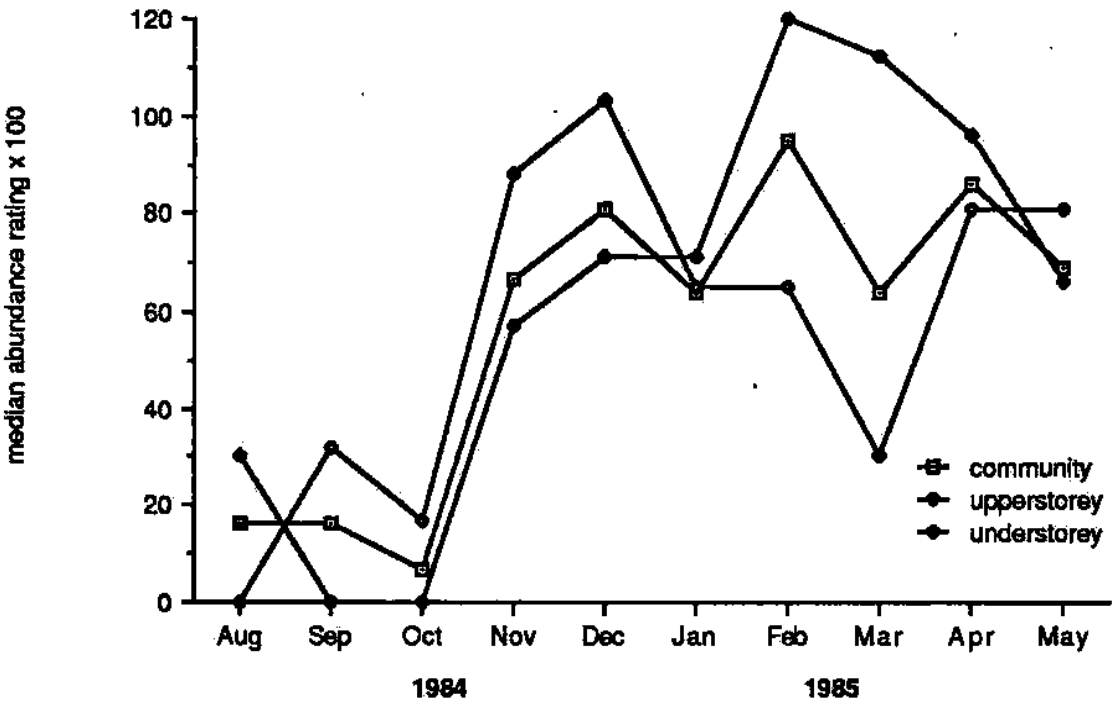
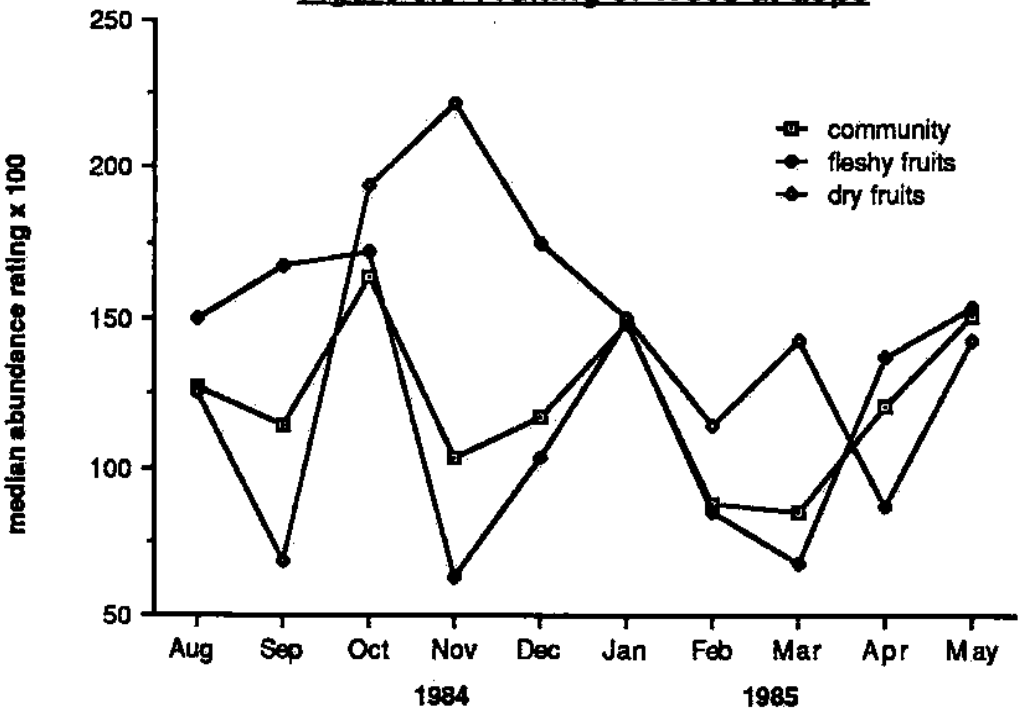


Figure 3.6 Fruiting of Trees at Lope



abundance ratings = 0-4 Scale
where ∅ = no flowers/fruit
1 = 25% potential production
2 = 50% " "
3 = 75% " "
4 = 100% " "

was unknown. Although estimates were available from Costa Rica (Glander, 1975) and Sarawak (Whitmore, 1984), in was not possible to extrapolate from these data without more detailed information, as sex-ratios in dioecious species are skewed (Bawa & Opler, 1974).

Accurate quantitative measures of fruit crops were beyond the scope of this study, given the difficulties of sampling fruits on individual trees. Previous studies have described seasonal variations in fruit production, but only a few have separated species into classes based on their morphology, and hence agents of dispersal (e.g. Alexandre, 1980; Lieberman, 1982; Sabatier, 1985). At Lope 73.6% were fleshy, 18.9% were wind dispersed, and 7.5% were dehiscent.

Figure 3.6 illustrates the fruiting of the entire sample, and of 2 subsets of trees: fleshy-fruiters, and dry-fruiters. Community peaks occurred in October 1984, January and May 1985. Fruit production was not correlated with rainfall. Different patterns were observed between fleshy-fruiters and dry-fruiters. Fleshy-fruit production varied considerably, peaking 3 times, as described for the community as a whole. Dry-fruits, which were wind dispersed or required reduced humidity for dehiscence, showed the biggest amplitude in production. Figure 3.7 shows the intensity of fruiting: in August and November fewest species fruited, but they produced large crops; in January, February, and May many species bore fruit in small quantities.

Fruit development may take up to a year after flowering, and maturation within 4 months is considered rapid (Opler et al, 1980). The duration of fruiting at Lope was variable, depending not only on ripeness, but on fruit palatability to a range of consumers. Panda oleosa fruits remained on trees for 5 months and were only eaten by elephants and ruminants once they dropped, whereas Nauclea didderichi and Ficus thonningii trees were stripped of their fruits by primates and birds within days of ripening. When fruiting was extended peaks in abundance were not obvious, as in Cola lizae and Duboscia macrocarpa. Statistical tests for co-ordination of activity require at least 10 individuals (D.M. Newbery, pers.comm.). The only species which met this criterion fruited in early 1984, before the collection of quantitative data began. A qualitative assessment suggested that 38.0% species (19) were synchronous, 2 species

Figure 3.7 Intensity of Fruiting by Trees at Lope

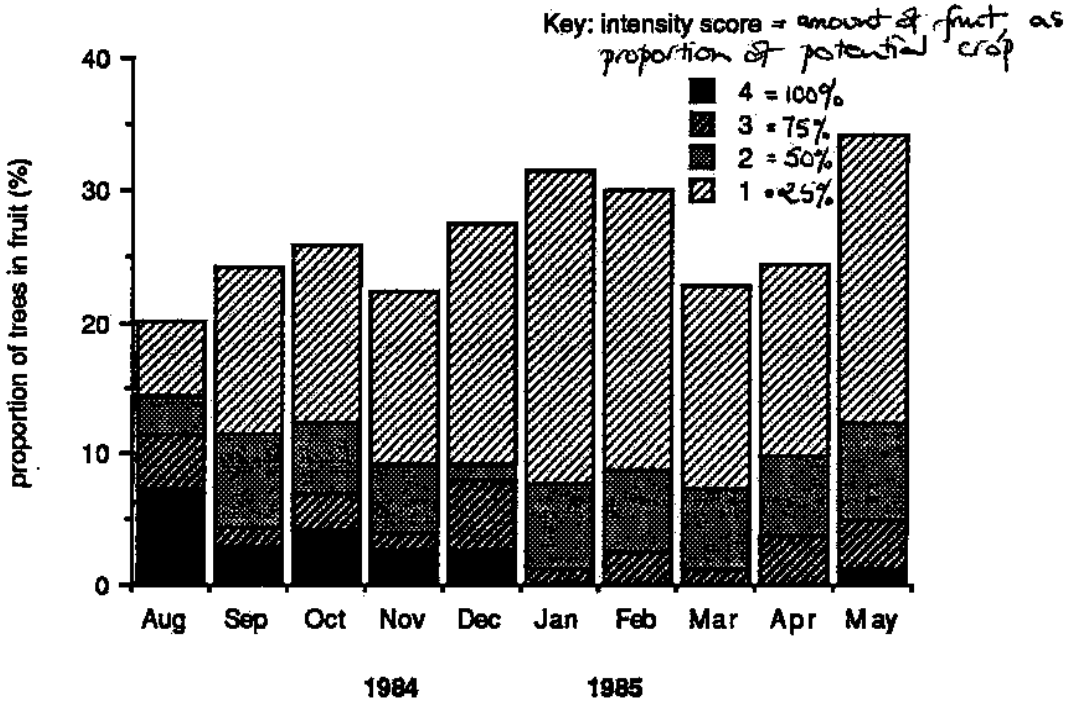
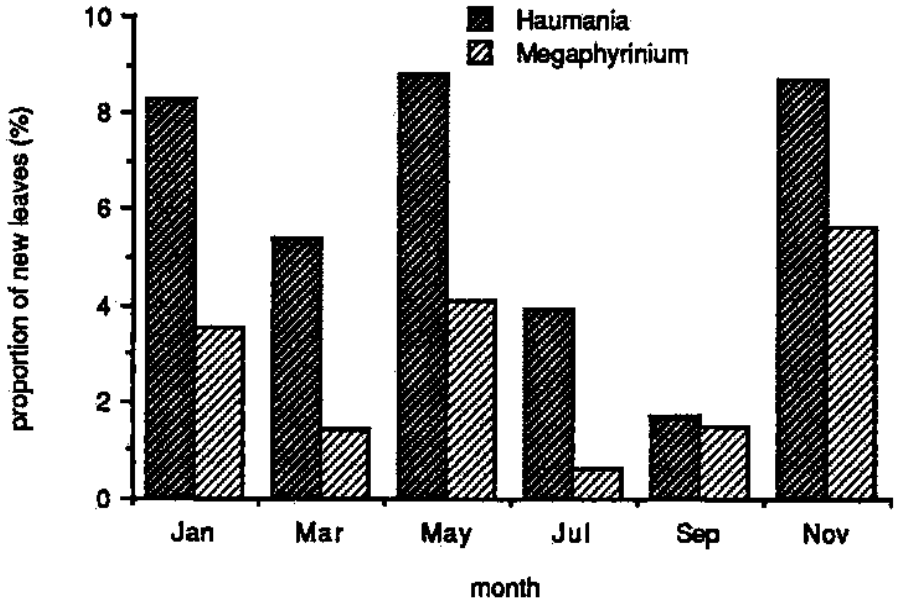


Figure 3.8 Marantaceae Phenology



were asynchronous (Hexalobus crispiflora and Pseudospondias microcarpa), while 29 could not be determined.

2. Phenology of Herbs

Both the fruits and stem-pith of Aframomum were sources of food for gorillas. Although the reproductive activity of Aframomum generally peaks during the wet seasons, the production of new shoots is continuous (Bullock, 1981; Hopkins, 1970), thus stems were continuously available as a source of forage. At Lope ripe Aframomum fruits were available for the first 6 months of 1984, but scarce for the remainder of the study as a result of the ill-defined dry season. A few flowers were observed during September 1984, but hardly any fruits developed. Only unripe seeds were found in gorillas' dung, in January and February 1985.

The Marantaceae could not be identified to species level in the absence of reproductive parts, thus they were lumped into two classes: Haumania-type and Megaphrynium-type. The production of young leaves was biannual: it was minimal in September (the major dry season), peaking in November and May (the wet seasons) (Figure 3.8). The seasonal differences in new-leaf production were statistically significant in both groups (Megaphrynium: $F= 7.07$, $p<.001$; Haumania: $F= 6.98$, $p<.001$), but the correlation with rainfall for the previous months at Lope was significant for Megaphrynium only (Megaphrynium: $r(6)=.9325$, $p=.007$; Haumania: $r(6)=.7624$, $p=.078$).

3. Inter-Annual Variation

There were many differences between 1984 and 1985, both in overall production and in the particular species which fruited. Several important gorilla foods, Celtis tessmannii, Cola lizae, Heisteria parvifolia, Maranthes gabunensis, Santiria trimera and Zanha golungensis, produced abundant fruits from January to May 1984, before the collection of systematic data began; June to July 1984 was a Dialium 'season'. However, none of these species fruited again until 1986 (C. Tutin, pers.comm.).

Fruit crops are generally larger after well-marked dry seasons (McClure, 1966, Medway, 1972, cited in Alexandre, 1980), and bizarre climatic events can upset phenological patterns to such an extent that 'frugivore famines' ensue (Fleming, 1982b).

Unusual conditions occurred in Gabon in 1984, when rain fell during the long dry season. Rain and wind can damage fragile reproductive structures and cause fruit to be aborted (Gautier-Hion et al, 1985a). Insect predation can also directly affect fruit crops, for example, Celtis tessmannii at Lope produced copious flowers in November 1986 for the first time in 3 years, but these were ravaged by caterpillars (C. Tutin, pers.comm.). Tutin also reported that early 1984 was unequalled until 1987, in terms of fruit abundance.

4. Discussion & Conclusions

Seasonal rhythms of productivity are well known in tropical forest (e.g. Foster, 1982a), but at Lope some cycles were disrupted by rainfall during July and August 1984. In general the production of flowers peaks at the end of the long dry season (e.g. Croat, 1975; Sabatier, 1985); leaf renewal is maximal at the beginning of the wet seasons, and minimal during the long dry season (e.g. Gautier-Hion, 1983; Hladik, 1978). Fruiting tends to peak in November and December, and is reduced during July and August, as seen in the Ivory Coast (Alexandre, 1980), in north-east Gabon (Gautier-Hion et al, 1985a) and in Guiana (Sabatier, 1985).

The production of new leaves, flowers and fruits tends to peak biannually. Leigh (1982) stated that rainfall emerges as the physical variable whose fluctuation is most decisive in the life of the forest. Rainfall is the cue for flowering, if the preceeding drought has been sufficiently intense (Augspurger, 1982), and water stress may constrain the maturation of fruit (Gautier-Hion et al, 1985a). At Lope phenological patterns were influenced by rainfall, but few significant correlations were found, due to the unusual pattern of rainfall in 1984.

Variation between years is well known (e.g. Gautier-Hion et al, 1985a), with individual trees fruiting at intervals of up to 10 years (Raemaekers et al, 1980). Only 60% of species sampled at Lope fruited during 8 months, but this observation was not unusual. For example, in Malaya only 33% of species studied fruited in 1 year (Raemaekers et al, 1980), and in Guiana less than 50% fruited in 2 years (Sabatier, 1985).

At Lope both individual fruiting patterns and overall production differed between 1984 and 1985, however it was clear that fruits were abundant for short periods and scarce

during others.

D. FOOD AVAILABILITY

1. Density & Distribution of Food-Trees

At Lope many food-trees were relatively rare: 25.7% (N = 9) of the species which were recorded on transects occurred at densities lower than 1 per hectare. A simple indicator of food available to gorillas was the proportion of food-trees in the population. Adult trees were classified as those which had attained at least 30 cm dbh (cf. Hubbell & Foster, 1986). Exceptions to the rule were 2 species which produced fruit below this threshold: Pausinistalia macroceras and Porterandia cladantha, and adjustments were made accordingly. Food-species were divided into 'major' and 'minor' foods, depending on whether their contribution to the fruit diet of gorillas was more or less than 1% by volume (see Chapter 4). Table 3.6 shows that approximately half of the population consisted of potential food-trees, but this may give the erroneous impression that food was abundant. The estimates included an unknown proportion of non-fruit-bearing male trees of dioecious species (see above). Also, the limited temporal availability of fruit has not been taken into account: no more than 21.1% individuals produced fruit in any one month, therefore less than 12.5 trees per hectare bore fruit at any one time.

Table 3.6 Proportion of Food-Trees in the Population at Lope

	'Major' species (N = 14)	'Minor' species (N = 21)	Cola (N = 1)	Total (N = 36)
proportion of population	4.8%	21.3%	25.6%	51.6%
prop. of adult population	10.3%	20.2%	15.4%	45.9%
number of adult trees/ha	13	26	20	59

Comparative estimates range from 3.5 trees in fruit per hectare in north-east Gabon (Gautier-Hion et al, 1981) to 45-58 trees per hectare in Sumatra (Whitten, 1982). Tree-size and individual yields have not been taken into consideration, the next section, however, provides more quantitative information on food availability.

2. Fruit-Availability Index

I devised an index to provide a relative measure of fruit availability, and to highlight variation in production between months:

FAI = E (mean FR 'major' x IV) + E (mean FR 'minor' x IV x 0.5)

where:

E = sum of

FR 'major' = fruiting intensity for each 'major' food-species

FR 'minor' = " " " " 'minor' " "

IV = Importance Value for each species

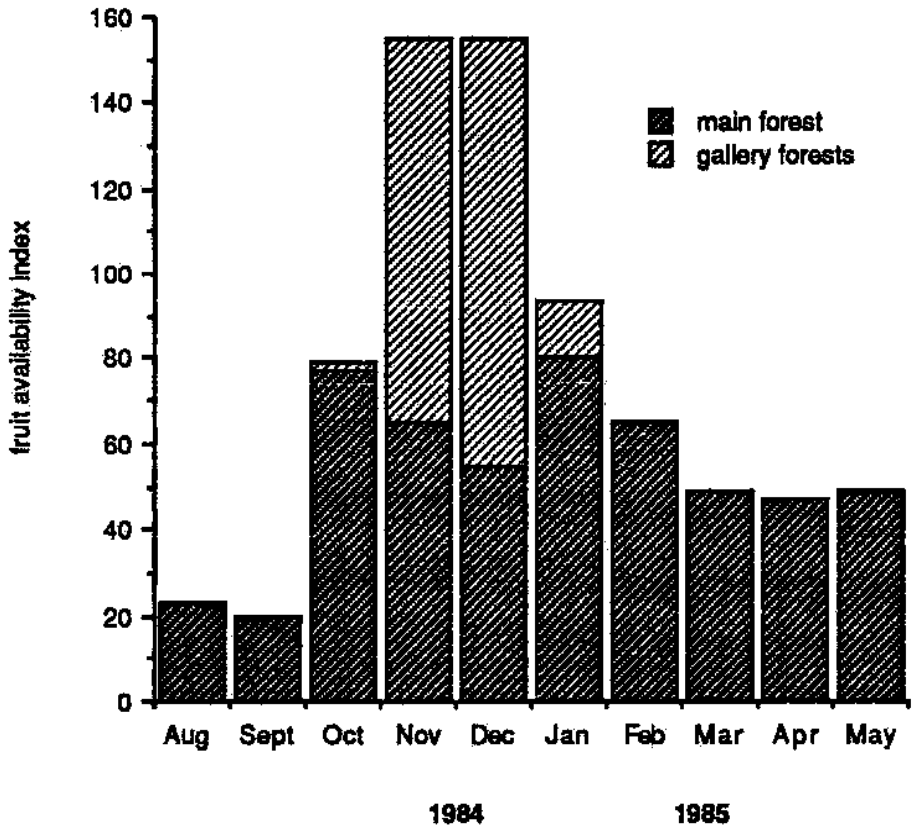
Aldrich-Blake (1978) stated that estimates of food availability are of little predictive value regarding primates' use of resources. Other factors, such as food quality, also operate on individual food selection. Thus my rationale for excluding non-foods from the FAI was to assume that gorillas were good judges of food content, and were likely to avoid items which were incompatible with their digestive physiology. The FAI was restricted to fruit, as knowledge of the other food-types eaten by gorillas at Lope was limited.

When phenology data were not available for a particular species during a given month, fruit production was estimated from information in the field-notes, and corroborated by the appearance of seeds in the gorillas' dung. The FAI was based on fruiting intensity, that is, phenology scores, and not on proportion of the canopy bearing fruit, or on crop-size. Fruit and leaf production of a given species is generally proportional to canopy size, which is correlated with dbh (e.g. Hladik, 1978; Oates et al, 1980), so Importance Values were incorporated as measures of species' density and basal area (see above). IVs were predicted for 3 food-species which did not occur on the transects (Parkia bicolor, Uapaca guineensis and Scytopetalum klaineanum) from their distribution outside the areas sampled.

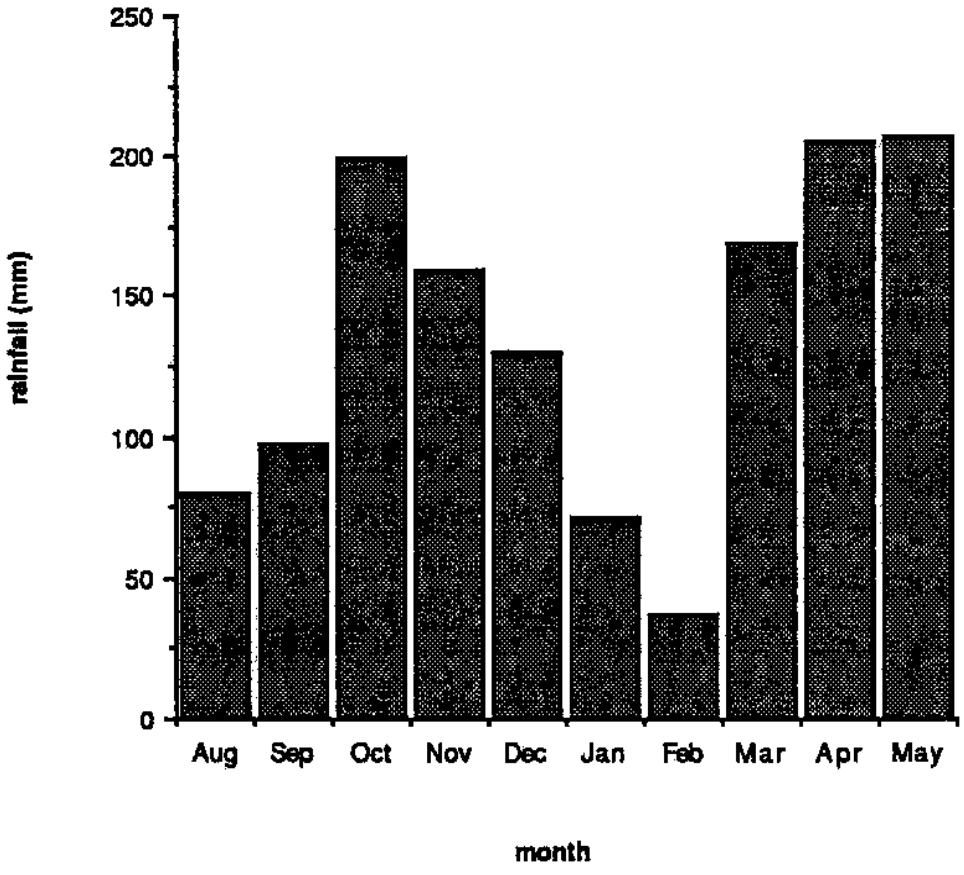
A threshold of 30 cm dbh limited the number of immature, hence non-fruit-producing trees, included in the estimates, with exceptions made for 2 species: Pausinistalia macroceras and Porterandia cladantha, as mentioned above. It was not possible to adjust

Figure 3.9 Fruit Availability Index (FAI)

see p36 for explanation



Rainfall at Lope (monthly totals)



for male trees of dioecious species, however individual trees were selected at random, and all were included in the calculations of means.

A mean fruiting intensity was derived for each species for each month, and adjustments made for unripe and inedible fruit, which were apparently unpalatable to gorillas. Given that the FAI was a measure of potential rather than an actual measure, factors such as parts discarded by gorillas and fruit-size were excluded. 'Major' and 'minor' foods were defined according to their contribution to the gorillas' diet, and thus independently from their abundance in the habitat. The index was weighted by reducing the contribution of minor foods by half. Such seemingly arbitrary ratios can produce useful and realistic measures, as demonstrated by Sailer et al (1985).

The FAI was intended to be a better predictor of the gorillas' feeding than the data on fruiting phenology for the community as a whole, particularly as several species were not added to the phenology sample until their importance as food-items had been demonstrated. This was corrected for in the FAI. Thus the FAI was measure of food-tree abundance in the population and the production of fruit by those trees. Quantitative phenology data were not available before August, thus FAIs have been calculated for 10 months only. Figure 3.9 shows that fruit-foods were relatively scarce during the long dry season, in August and September, and relatively abundant throughout the major wet season, from October to January.

3. Aframomum & Marantaceae Biomasses

The pith of Aframomum fronds and the bases of young leaves of Marantaceae were weighed to estimate the amount of food available to gorillas per unit area. This was found to be at least 230 kg potential food per hectare (Rogers & Williamson, 1987). Watts (1984) provided comparative data on the biomass of THV available to mountain gorillas: stem densities and the frequencies of 'food-less' patches were similar in both habitats, but the biomass of herbaceous food was about 4.5 times greater in Rwanda (Table 3.7).

4. Other Food-Types

Gorillas also ate the fruits of 5 species of shrubs in the forest understorey and the

savannas (Antidesma vogelianum, Psidium sp., Psychotria peduncularis, Psychotria vogeliana, and Cissus sp.). Their production was not quantified. One of these, Psidium, fruited biannually, but patterns were not discerned in the other species.

No specific measures of leaves as food were taken, but overall production of leaves peaked in November, at the beginning of the rainy season, as shown above.

Table 3.7 Biomass of Herbaceous Foods of Gorillas in Gabon and Rwanda

	LOPE	MT. VISOKE
proportion of 1 m2 quadrats which contained food	89.4%	82.6%
number of stems/m2	7.7	8.8
biomass of foods/m2	366g	1,650g

---

5. Discussion & Conclusions

At Lope many food-trees were relatively rare, although a large proportion of the population consisted of potential food-trees due to the high density of Cola. However fruits were produced for limited periods only, and on average less than 12.5 trees per hectare would have been in fruit at any one time. An index of availability showed that seasonal variation in the abundance of fruit-foods was striking. The herbaceous Aframomum and Marantaceae, which were important to the gorillas, were found to be ubiquitous. The production of new leaves by these herbs also peaked in the major wet season.

Calvert (1985) estimated that foods in mature forest occurred at low densities. However, she proposed that as some food was present in 70% of quadrats, mature forests were good insurance against finding no food in fields or along stream-banks. The patchy distribution and marked seasonal availability of gorillas' foods in lowland tropical forests contrast with the abundance of food in eastern gorillas' habitats. The only changes in food availability at Mt. Kahuzi were the seasonal growth of bamboo, and the production of 2 species of fruits (Casimir, 1975). In montane forest food for folivores is adundant, but fruits are rare (Fossey & Harcourt, 1977). The low density of trees allows

the ground vegetation to flourish (Goodall & Groves, 1977), and the biomass of herbaceous food is almost 5 times greater in Rwanda than at Lope. Both Vedder (1984) and Watts (1984) systematically sampled food availability in the Virunga volcanoes. Neither found any evidence of seasonality in the foods of mountain gorillas, and Watts concluded that restrictions on the availability of specific food-items were minor, although he recorded seasonal changes in the rates of growth. He also stated that "It is the relative unimportance of temporal fluctuations in food availability, as much as the extent of spatial variability in food and habitat quality, that distinguishes the ecological circumstances of mountain gorillas from those of other primates" (1984:351).

E. SOME FACTORS AFFECTING THE VEGETATION

Disturbance may be the most important factor causing variation in vegetation (Whitmore, 1984) and this may arise from several sources, some of which are considered below.

1. Selective Logging

The Lope falls within the limits of Aucoumea klaineana distribution and the study-area was exploited for wood until the late 1960s. Extraction took place at a low level with 'minimal' disturbance to the forest, but even logging selectively can have profound effects on the vegetation structure. Damage is caused to trees neighbouring that which is felled, by hauling out logs, and by road contruction. According to Calvert (1985) single trees created 0.04 hectare gaps when felled. In areas of West Malaysia where logging occurred at 18 stems/ha up to 51% of trees were damaged in the process (Johns, 1986), and felling 10% trees may destroy 55% of the surrounding trees (Burgess, 1971, cited in Wilson & Wilson, 1975). However, the apparent 'secondarisation' of the Lope forest extends far beyond those areas which were accessible to the foresters, thus logging has not been responsible for producing the structural characteristics of most of the forest at Lope.

2. Tree Falls

Tropical forest is intrinsically dynamic and a high frequency of tree falls allows

increased development of the understorey. The turnover rate due to the mortality of trees in north-east Gabon led to a 10% change in the population of trees over 7 years (Hladik, 1982, 1984). There may be a 'domino effect' of falling trees: at Lope 6 large trees were brought down in the wake of a single dead one. Many trees fall during storms with gusty winds at the beginning of the rainy season (Alexandre, 1980; Brokaw, 1985b). Rain loosens the soil around tree roots, but 75% of tree falls in north-east Gabon were caused by the increased weight of water on the trees' surfaces (Florence, 1981). Tree falls are also caused by elephants (Leigh, 1975; Whitmore, 1984). Tree falls create light gaps, which play a vital role in regeneration and the maintainance of diversity in tropical forests (e.g. Hartshorn; 1980; Richards, 1983). At Lope fallen branches formed 'log-jams' in streams, with consequent changes in the courses of streambeds. Also, blockages on paths caused by fallen branches or trees led to diversions, and the creation of new paths by large mammals.

3. Elephants & Gorillas

After humans "no other animal has had as great an effect on African habitats" as the elephant (Laws, 1970). These 'bulldozer herbivores' (Kortlandt, 1984) cause damage by browsing, stripping bark, breaking, uprooting, and trampling the vegetation. At Lope forest elephants, Loxodonta cyclotis, were present at high densities during the wet seasons. They seemed to be particularly attracted to light gaps with regenerating vegetation. Immediately after a tree fall they stripped the newly accessible leaves and bark, flattening the surrounding area in the process, and fed on new growth as it emerged. Elephants can thus maintain the early seral stages of developing plant communities (Wing & Buss, 1970), or they may deflect succession and cause dominance by particular tree species (Laws, 1970). They can also prevent the expansion of forest by debarking, which renders mature trees more susceptible to fire (Eggeling, 1947; Wing & Buss, 1970).

The effects of gorillas on their habitat were not as devastating as those of elephants, although they broke branches from trees, snapped saplings in two, and flattened areas of vegetation. But they did not generally uproot herbaceous plants in the same way as

elephants. Because gorillas were also able to climb, their influence on large trees was apparent: female trees of the dioecious Uapaca had a pruned appearance after fruiting. Similarly, Rijksen (1978:96) observed that some trees looked "battered" months after orang-utans had fed in them.

Mention should also be made of the gorillas' influences on their food-plants: if browsing stimulates the production of immature growth (young leaves, stems, and apical tissue) it will be beneficial to the gorillas, by increasing the availability of food. Aframomum plants recovered rapidly from primate herbivory and Bullock (1981) proposed that such action may stimulate regeneration, resulting in increased shoot emergence. Mountain gorilla-induced structural damage increased the productivity of several important food species: stem densities and growth rates were higher 6 months after patches had been used by gorillas (Watts, 1987).

Both gorillas and elephants may be important dispersers of seeds. The passage of seeds through the digestive tracts of elephants (Lewis, 1987) and several species of primates is thought to enhance germination (e.g. Estrada & Coates-Estrada, 1986; Garber, 1986; Gautier-Hion, 1984), and similar claims have been made for 3 species of great apes (bonobos: Idani, 1986; chimpanzees: Takasaki, 1983; orang-utans: Galdikas, 1982). Jones and Sabater Pi (1971) proposed that a mutualistic relationship existed between gorillas and Aframomum plants, but such relationships are rare (Lieberman & Lieberman, 1986).

Gorillas at Lope were important consumers of fruit, and hence determined the fates of large quantities of seeds. Many seeds passed through the gut intact, and presumably unharmed. Large numbers of seedlings of several species sprouted from the gorillas' dung (e.g. Celtis tessmannii, Cola lizae, Santiria trimera, Parkia bicolor, and Zanha golungensis), but many seedlings would be "doomed to intense competition in faecal clumps" (Howe, 1980:944).

Seeds may be subjected to a chemical or mechanical action in the gut which is beneficial to germination (e.g. Estrada & Coates-Estrada, 1984). Preliminary trials indicated that ingestion by gorillas increased the proportion and rate of seed germination (A. Feistner, pers.comm.). The gorillas' large digestive tract, long gut

passage time, and large ranges, would result in seeds being transported considerable distances away from parent plants, which is an important aspect of dispersal. Also the dung matrix would reduce dessication of seeds, and provide a suitable substrate for germination.

The term "animal dispersal" may have become synonymous with the swallowing of seeds (Smythe, 1986). Lieberman and Lieberman (1986) accepted that fruit ingestion accomplished dispersal, but they stated that this was the only clear benefit of endozoochory, and that germination enhancement was neither inevitable, nor common. Although caution must be taken before concluding that gorillas are reliable, high quality dispersers, an example of the vital role of dispersers was given by Alexandre (1978): some species of trees no longer regenerated effectively in areas of the Ivory Coast where elephants had been hunted out. Among the tree species affected were Pentadesma butyracea and Saccoglottis gabonensis, which were also eaten by gorillas at Lope. Lieberman et al (1987) suggested that only elephants could swallow the large seeds of Klainedoxa intact, but Klainedoxa gabonensis were ingested by the Lope gorillas. Thus it seems likely that gorillas are important seed dispersers.

4. Savannas

The Lope forest is bordered by savannas, which are burnt annually during the long dry season. Humidity, temperature, and lumination may be altered at the interface between the 2 habitat types, and such peculiar conditions might favour the growth of herbaceous vegetation, deciduous and pioneer tree species. Savannas provide an invasion front for pioneer species (Whitmore, 1984), which may thus achieve unusually high densities, as seen in the case of Cola lizae.

F. DISCUSSION & CONCLUSIONS

The Lope may not be 'typical' of tropical forests, but as Harrison (1984:7) remarked "The heterogeneity of rainforest...may leave little to be gained from attempting to characterise the Lope forest as 'typical' or 'atypical'". Hladik (1973) described the M'passa forest of Gabon as having a "particular" structure, with a low tangled canopy,

few large trees, and some characteristics of open forest, giving the impression that it was secondarised. But that area had never been logged or cultivated, all disturbances were natural.

The significance of Cola lizae, a new species of tree discovered during the course of this study (Halle, 1987), is not yet understood. Cola may occupy the niche which is filled by the pioneer Musanga cecropioides in other regions of Gabon (A. Hladik, pers.comm.). Cola occurred at high density, but 'pioneer' species are integral to all stages of development in tropical forest communities (Knight, 1975), and were present in the 'virgin' forests of north-east Gabon (Aubreville, 1967). Saccoglottis gabonensis was also found at Lope, yet this is a coastal species, which had not previously been recorded so far east. A further indication that this ecotope is unusual is that normally savanna-dwelling species of birds can be seen up to 1 km into the forest (C. Henty, pers.comm.).

The presence of herbaceous vegetation has been taken to indicate disturbed forest, and the opulent herb layer at Lope may be unusual, but a lack of understanding of tropical forest dynamics has led to erroneous classifications of forest types (Hartshorn, 1978). The Lope seems to be a special ecotope, resulting from an interaction of several major influences, including the mammalian fauna, the peripheral savanna, and selective logging. The complex factors which shape forests are only partially known and barely quantified.

The forest at Lope was found to be similar to other areas of tropical forest, in terms of species densities and diversity. The spatial distribution of tree species was characteristic of heterogeneous tropical forests: individuals were widely separated and some were clumped, which was important from the gorillas' view-point. The production of new leaves, flowers and fruits was seasonal, although patterns of phenology seemed to have been disrupted by the abnormal distribution of rainfall during 1984. An index of fruit availability showed marked fluctuations. The diversity and seasonal abundance of fruits provided a major source of food. Montane forests, in contrast, show no evidence of seasonality in food abundance, and fruit production is extremely low. The present study confirmed that there are few similarities between the lowland gorillas' tropical forests and the mountain gorillas' montane habitat.

CHAPTER 4 : FEEDING

A. INTRODUCTION

In the last decade several papers have described correlations between the ecology and morphology of a wide spectrum of primates (e.g. Milton & May, 1976; Clutton-Brock & Harvey, 1980), with body size and dietary quality among these factors (e.g. Sailer et al, 1985; Kurland & Gaulin, 1987). Almost without exception, information concerning gorillas in these analyses were based on extrapolation from the excellent data available for the folivorous mountain gorilla, Gorilla gorilla beringei. To surmise that gorillas in lowland tropical forest will consume equivalently large proportions of foliage, given the diversity of fruit available, is surely presumptuous. This notion was not challenged until recently (Tutin & Fernandez, 1984), despite previous portrayals of lowland gorillas as fruit eaters (e.g. Sabater Pi, 1966b; Yerkes & Yerkes, 1929:539). An inventory of gorilla foods from Equatorial Guinea listed 52 fruit species (e.g. Sabater Pi, 1977). The apes' propensity to feed in plantations and secondary forest has been well publicised (e.g. Derochette, 1941; Liz Ferreira et al, 1949; Petit, 1920). This may be because such areas are associated with human habitation, and thus more easily accessible to observers. The image of the gorillas' tendency to use light gaps and other areas of dense heliophyllic vegetation was enhanced by Calvert's (1985) study, which drew attention yet further away from the majority of gorillas inhabiting mature forest.

Also it has been asserted that adult gorillas' access to fruit is restricted as a consequence of their poor climbing ability (e.g. Dyce-Sharpe, 1927; Sabater Pi, 1977). This is not true, as even silverbacks are capable of climbing and do so frequently at Lope (see Chapter 6). This chapter describes the frugivorous nature of Gorilla gorilla gorilla, using data from 277 trails, 716 dung samples (190 kgs) and direct observation of feeding on 60 occasions.

1. Feeding Trails

Feeding trails are the remains of food *in situ*, and may indicate gorillas' patterns of movement. Traces were recognisable by the characteristic manner with which each

food-type had been processed, and the particular plant parts discarded. Qualitative information was recorded, that is, the species fed on and the parts removed, but quantitative data on the number of items eaten were not collected, as the priority at the time was to catch up with the gorillas. Generally such detail would have been of little use without complementary information on group composition, and the time gorillas spent at each location. For these reasons all trails discovered in one area in any one day were treated as an entity for the purposes of description. Many trails could only be followed for short distances, 100 m or so, and did not provide evidence of a complete day's travel or feeding routes.

2. Evaluation Of Dung

Several researchers have examined primates' faeces to identify species consumed (e.g. Goodall, 1974; Nishida & Uehara, 1983; Calvert, 1985; Sugiyama & Koman, 1987), although Casimir (1975:110) stated that such investigation "merely confirmed" information gained from trails. Suzuki (1969) estimated the proportion formed by each food-class by volume, but he conceded that these percentages were not absolute. Hoshino (1985) recorded the frequencies of each food to measure qualitative variation in the diet of mandrills, and he attempted to quantify each food category by dry weight for a subset of samples.

Relying to a large extent on macroscopic faecal analysis leads to a bias against soft plant parts and those parts which are reduced to fine particles by mastication or digestion. Quantifying data from dung is problematic, as not all items eaten are equivalently represented in the corresponding residue (Moreno-Black, 1978), and the digestability of specific foods varies according to the other constituents of a meal (Putnam, 1984). Detailed information was collected on parts identifiable in the dung, such as seeds and fruit skins, but fragments of leaves and stem-fibre, which became an indistinct mass, were assessed simply by scores of relative abundance.

At Lope the average weight of all dung samples was 268g, dung of adult males only was 707g. Goodall (1977) reported that silverbacks produced 30 kg dung per day. If this estimate was appropriate to lowland gorillas, then even the largest sample collected

(2700g) formed less than 10% of an individual's daily output. However, 42.2% of the dung samples came from nest-sites, where Schaller (1963:203) reported that half the dung was deposited, so the large sample may have been as much as 50% of the daily output. In either case, therefore, a single dung sample may not have contained remnants of all food-types eaten during the previous 24 hrs.

3. Calculation Of Relative Fruit Volumes

As no soft parts remained in the dung, the volume of seeds and other undigested parts excreted was not representative of fruit intake. For a more realistic evaluation of fruit contribution to the diet I calculated the volume of fruit consumed. This was estimated retrospectively from seeds in the dung (see Figure 4.1). For each species the volume of an individual fruit and of the seeds within it were estimated by various means: direct measurements of fruit specimens; scaled photographs and measurements from drawings made in the field; information from botanical volumes and foresters' identification manuals. These estimates were then corroborated by other field workers at Lope. Volumes were calculated using the formula for an elipsoid (also appropriate for a spheroid), as most seeds approximated to this shape:

$4/3\ \Pi\ (ab^2)$ or $4.189\ (ab^2)$, where a = length x 0.5, b = width x 0.5, a > b

The volume of pulp was obtained by subtracting seed volumes from the fruit volumes. Two measures were used, one to estimate the relative amount of fruit consumed, the other to indicate what fraction of this fruit was 'utilisable', thus two factors were allocated to each species:

F1 = volume of fruit ingested per seed

F2 = " " pulp " " "

This process was more complex for 14 species with (i) large numbers of small (1 mm) seeds (e.g. Ficus, Nauclea); (ii) for small fruits eaten in large numbers (e.g. Psychotria); and (iii) for species sometimes recorded as pulp only (e.g. Pentadesma). These species were represented by relative abundance scores, and F1 and F2 were estimated for a 'standardised' faecal sample of 250 g. For simplicity 'abundant' was taken to represent twice the value of 'common', 4 times that of 'few', and 8 times that of

'rare'.

The sum of the volumes of all species in each sample was divided by the weight of that dung sample to provide a comparative measure, which approximated to cm^3/kg. Volumes of both the relative fruit consumed (RFC) and the relative pulp consumed (RPC) are presented below. Dung for which fresh weights were not available were removed from analyses. Also excluded was dung collected outside the main study-area, in forest with a slightly different species composition and phenology, which could not be related to phenology data. A reduced sample of 629 faeces and 56 recognisable types of fruit formed the core of the data. Appendix 4.1 lists the 56 fruit species with their F1 and F2 values.

Two important assumptions were made in calculating fruit volumes: (i) that a typical size and shape of fruit could be ascribed to each species; some fruits contained increasing numbers of seeds in relation to their size, but reliance on seed counts reduced some of this inherent variation. It was also assumed (ii) that all seeds were swallowed, which was not the case; notable exceptions are mentioned below. Although no compensation was made for such species, some volumes were estimated from undigested pulp, rather than seed counts. Nonetheless, fruit volumes may have been slightly underestimated.

B. COMPOSITION OF THE DIET

At Lope 139 different plant parts of at least 103 plant species (92 identified) from 26 families were included in the diets of 9 groups of gorillas during 17 months. In addition to vegetable matter, at least 6 species of invertebrates, earth, water, and possibly dung were ingested. Appendix 4.2 is a complete list of species, which has been summarised in Table 4.1.

1. Structural Plant Parts

a) Monocotyledons.

The herbaceous component of the diet, comprising 29 items (or plant parts) from 20 species, was dominated by 2 families: 10 species of Marantaceae, and 5 species of Zingiberaceae, including Aframomum. Aframomum is a name that has been almost

Table 4.1 Composition of the Diet of Gorillas at Lope

FOOD-CLASS	FOOD-TYPE/LIFE-FORM	N	PARTS EATEN	N
Fruits	medium-large trees	47	pulp	54
	small trees	4	seed	7
78 species	shrubs	5	aril	5
	vines	6	entire fruit	1
78 items	herbs	8	indet.	11
	unknown	> 8		
THV	Marantaceae	11	leaf-bases	7
	Zingiberaceae	> 5	stem-bases	7
20 species	Commelinacea	1	leaves	3
	Acanthacaceae	1	stems	6
29 items	Araceae	1	pith	6
	Palmaceae	1		
Leaves	trees	12	leaf tissue	19
(Dicotyledons)	saplings	3	petioles	> 2
22 species	shrubs	2	bracts	> 1
	vines	2	new shoots	> 1
23 items	unknown	> 3		
Bark	tree	3		
	shrub	1		
5 species	unknown	> 1		
Insects	ants	> 3		
6 species	indet.	3		
Miscellaneous	flowers	> 1		
	roots	> 1		
5 items	wood	> 1		
	vine tendrils	> 1		
	soil	1		

TOTAL: Number of Identified Species = 94 (including 2 insect)
Number of Plant Species = > 103
Number of Plant Food-Items = 139
Number of Items in Diet = 146

synonymous with western lowland gorillas since 1847 (Savage & Wyman), not least because of the "mutualistic relationship" hypothesised by Jones and Sabater Pi (1971). Aframomum is a major food for populations of gorillas in Cameroon (Butzler, 1980; Calvert, 1985), Equatorial Guinea (Sabater Pi, 1977), Gabon (Tutin & Fernandez, 1985), and Zaire (Schaller, 1963:151).

At Lope 98.3% of the dung contained stem-fibre, which was scored as common or abundant in 76.5%. The majority of trails included remains of Aframomum (81.9%) and Marantaceae (76.9%). The only trails with neither Aframomum nor Marantaceae were those which crossed monospecific stands of Anisotes macrophyllus. Leaf fragments, recorded in 90.1% dung, came from a combination of life-forms (trees, shrubs, vines, and herbs), but only Marantaceae were common on trails. Haumania was predominant (as in Campo, Calvert, 1985), plus Hyselodelphis and Megaphrynium. An unusual aspect of the gorillas' feeding was their ingestion of 3 species of semi-aquatic Marantaceae: Marantochloa cordifolia, M.purpurea, and Halopegia azurea. Patches of flattened herbs and split-stems were found in streams and marshes (see Williamson et al. 1988). The gorillas of Kahuzi-Biega, in East Africa, fed on the basal parts of Cyperus (sedge), and have been seen wading through brooks 60 cm deep (Casimir, 1975).

No simple relationship existed between the quantities of stems consumed and fibre in the dung, as there did between fruits and seeds, and without detailed observation, it was not possible to evaluate the precise contribution of Aframomum or of other structural plant parts to the gorillas' diet.

b) Dicotyledons.

Leaves from 19 species of woody plants were identified by observation or on trails. Most leaves came from trees and saplings (68.2%), and also from shrubs (9.1%) and vines (9.1%) (unknown = 13.6%). Petioles, new shoots, bracts, and vine tendrils were also eaten. Bark was recorded in 9.1% dung, usually in small quantities. It was eaten from 2 types of shrub and 3 trees, found on trails, of which Chlorophora excelsa was the most important. Wood and roots were also found in dung (N =18).

2. Reproductive Plant Parts

a) Flowers.

Feeding on Pterocarpus soyauxii flowers was observed only once. No remains were found in the dung, perhaps due to the delicate structure of flowers.

b) Fruits.

Fruit remains were recorded in 97.5% dung, including numerous pieces of fruits and seeds which could not be identified. Gorillas ate 78 species of fruit (67 identified) including one cultigen, the mango (Mangifera indica). Only 10.3% were herbaceous, 65.4% species came from trees, and 24.3% were unknown. About a quarter of species was recorded only once. The fruit diet was split into 2 categories, based on the relative proportions of fruit found in all dung samples:

(i) 'major' species:	> 1% RFC	N = 16
(ii) 'minor' species:	< 1% RFC	N = 39

Four species each formed more than 10% RFC: Cola lizae, Duboscia macrocarpa, Dialium sp. and Zanha golungensis. Only 2 of these, Cola and Zanha, plus Uapaca guineensis, formed equivalent proportions of the RPC, which is the utilisable (pulp) fraction of the fruit diet. Two additional species, Nauclea didderichi and Maranthes gabunensis, ranked highly for a single month, but failed to account for 1% of the overall diet. The mean RFC and RPC values for all species were 0.59 cm^3/kg and 0.25 cm^3/kg respectively.

Fruits were also categorised by quality. Four general fruit-types were identified from the published literature, and their principal chemical components determined (e.g. Sourd & Gautier-Hion, 1986; Rogers, in prep.). Morphological groupings tended to correspond with nutritional values.

(i) SUCCULENT FRUITS: generally brightly coloured, consisted mainly of sugars and water, most had low fibre and low secondary compounds, and were therefore easily digested; these formed the bulk of fruits eaten by gorillas, 34 species and 90.9% RPC.

(ii) FIBROUS FRUITS: generally large, dull coloured, with dense flesh emitting an odour; contained high fibre, tannins, low nutrients, thus low digestability; 4 species, 7.7% RPC.

(iii) ARILS: brighly coloured thin fatty layer adhering to seeds, high concentrations of lipids; 4 species, 0.1% RPC.

(iv) SEEDS: relatively high protein content, rich in secondary compounds, low digestibility; 4 species, < 0.1% RPC.

(v) UNKNOWN: not classified as information was insufficient; 10 species, 1.2% RPC.

Fruits of the 56 species identified in the dung were sub-divided according to life-form. The majority were produced by trees (88.8% RFC came from medium or tall trees, >15 m tall; 3.1% from small trees <15 m). Herbaceous fruits, mostly Aframomum and small quantities of Marantaceae fruits, contributed 4.0% to the RFC. Fruits of shrubs and vines formed 3.6% RFC.

Importance Values (IVs) were calculated for some fruit species in the gorillas' diet (Table 4.2). IVs incorporated relative frequency, relative density, and relative dominance (i.e. proportion of months eaten, as a measure of distribution through the year) for each species (see Chapter 3). Relative frequencies were calculated on a monthly basis, totalled, and converted to percentages. This controlled for the variable number of faeces collected each month. The most important fruit species at Lope were Aframomum, Uapaca guineensis, Dialium sp., Cola lizae, and Zanha golungensis.

3. Non-Plant Foods

a) Invertebrates.

Evidence of insectivory by gorillas at Lope came from trails and 33.2% of dung samples; 31.1% contained hundreds of undigested heads of weaver ants Oecophylla longinoda; the other 2.1% included remains of one of 5 types of black ant, ticks, bees, or in one case a caterpillar. The ticks were larval forms of Amblyomma thollini, and were probably swallowed during grooming sessions.

The proportion of dung containing Oecophylla at Lope and containing termites in north-east Gabon (30.5%, Tutin & Fernandez, 1983b) was virtually identical. Data were not available to compare invertebrate biomasses at the 2 sites, but it seems likely that weaver ants and termites filled the same niche in the gorillas' diets.

Table 4.2 Important Fruits Eaten by Gorillas at Lope

SPECIES	IMPORTANCE VALUES
Aframomum spp.	28.8
Uapaca guineensis	24.3
Dialium sp.	22.1
Cola lizae	18.8
Zanha golungensis	18.8
Duboscia macrocarpa	18.7
Psidium sp.	12.3
Klainedoxa gabonensis	9.8
Celtis tessmannii	9.6
Porterandia cladantha	9.2
Pentadesma butyracea	9.0
Santiria trimera	8.2
Cissus sp.	7.0
Diospyros polystemon	6.4
Scytopetalum klaineanum	6.3
Heisteria parvifolia	4.4

(See Table 3.4 for calculation of IVs)

Ants are the predominant animal matter eaten by all primates at M'passa in north-east Gabon (Gautier-Hion et al, 1980), and Oecophylla comes closest to being the universal insect food for chimpanzees (McGrew, 1983). Many social insects can be exploited without much expenditure of energy, but Oecophylla are of added importance as they are found in convenient 'packets': they bind leaves together into compact, tennis-ball-sized arboreal nests, each containing about 5 g of eggs, larvae, and adult forms (Hladik, 1973). Although ants may be a regular part of the diet, they form a small portion in relation to plant matter: invertebrates, including weaver ants, formed 3-4% by weight of the annual diet of chimpanzees at M'passa (Hladik, 1973).

b) Earth.

Geophagy is common among East Africa populations of gorillas (e.g. Schaller, 1963:166; Fossey, 1983:52). At Lope evidence of soil ingestion came from knuckle-prints at salt-licks in the banks of streams (Figure 4.2). These licks were created by elephants, and developed through frequent visitation by many mammals, including buffalo, antelope, chimpanzees, and colobus monkeys. Soil from these sites had a high concentration of sodium (M. Harrison, pers.comm.). Geophagy was seen 3 times, and soil or gravel was found in 4.3% of dung, during 8 consecutive months (September-April).

c) Water.

Knuckle- and foot-prints leading to streams without crossing suggested that gorillas drank water, despite the high water content of many of their food-items (mean = 73%, Rogers, in prep.). Gorillas in Cameroon have been seen drinking from streams (Critchley, 1968), mountain gorillas also drank water (Fossey & Harcourt, 1977), and chimpanzees in Gabon drank more than once per day in the dry season (Hladik, 1973).

C. FOOD ACQUISITION AND PROCESSING

1. Food Gathering

a) Foraging On The Ground.

Foraging occurred at different paces, judging from the variable patchiness and

density of food remains on trails. Large areas of Aframomum were flattened in the vicinity of nest-sites, and many split-stems were found, suggesting that feeding was intense early in the day. Basins of dense herbs were riddled with trails of many ages, and even those from the same day were winding and tangled. Group members moved in parallel, sometimes spread over 100 m, and made 'tunnels' under clumps of Haumania vines. Food remains were concentrated on stream banks and along road edges, where Aframomum was abundant, and split stems were left in heaps. Feeding in Marantochloa marshes was similarly intense, as gorillas made convoluted paths through marshes with a soft muddy substrate, or moved down the middle of streams, in water about 30 cm deep, uprooting plants from both banks, for up to 500 m (Figure 4.3).

Such ambling styles of feeding contrasted with the 'travel-feed' mode. When many trees were in fruit the gorillas moved fairly rapidly between them, so that traces were sparse and inconspicuous, often single items separated by up to 100 m. These two paces of feeding resemble those described by Calvert (1985). Gorillas also crossed open savanna to feed on the fruits of shrubs, or to reach gallery forests where other fruit sources could be found (see Chapter 6).

b) Feeding In Trees.

Gorillas were observed feeding in medium to large trees during 17 contacts, at a maximum height of 30 m in a Pterocarpus soyauxii 35 m tall. The average height at which silverbacks fed was 20 m (N = 10, R = 12-30); for all individuals it was 16 m (N = 25, R = 8-30 m). Even trees which were not particularly large supported more than one adult gorilla. A group of 5 gorillas fed together in an Uapaca more than once, and 9 individuals were seen descending from a Zanha. There are previous records of infant gorillas feeding at heights of 40 m, blackbacks at 35 m, and silverbacks at over 20 m in Zaire (Goodall, 1977) and at more than 18 m in Cameroon (Critchley, 1968).

Both sitting and standing positions were adopted for feeding in trees. Small terminal branches were bent within reach, often without breaking them. Single fruits and leaves were plucked directly with the lips, or pulled off by hand and transferred to the mouth. Arboreal vines were pulled through the canopy and run through a closed fist, leaving a bunch of leaves in the fingers. Food was also collected from neighbouring trees. Both

left- and right-handedness was seen. Often adults broke off branches and backed towards the trunk or a major fork to eat their meals from a more secure position. One female propped herself between the two trunks of a Pentadesma butyracea tree while eating. Branches were subsequently dropped to the ground, some with fruit still on them. One lone male feeding on Dialium broke off at least 10 branches of about 3 cm diameter. Although the ground below fruiting trees was often littered with debris, no evidence of co-operative behaviour was seen, whereby juveniles or females throw food down to silverbacks, popular with some authors (e.g. Allen, 1931; Jenks, 1911; Valker, 1931).

Some fruit species were eaten both in the canopy and on the ground once fallen. Even assuming that only half of these were consumed arboreally, most fruits were gathered and eaten in trees (71.8% RFC). Gorillas were seen clutching 4 or 5 Cola pods against the chest with one arm, eating others with the free hand, and dropping the pods as they were emptied. More than an hour was spent in a single tree, feeding continously, and turning around or shifting position every few minutes. This contrasts with Watts' (1984) report that mountain gorillas were terrestrial during 96.2% of their feeding time.

A method employed by silverbacks feeding on small trees or saplings is illustrated by this extract from the field-notes: "The silverback climbs to 2 m, moving slowly and with great concentration and the sapling slowly bends until the trunk is horizontal. The gorilla stands quadrupedally for a moment and then lowers himself, gripping the trunk with one hand - the sapling bends and cracks and the gorilla keeps his hold as he reaches the ground". This technique was particularly destructive, especially in this instance, when the desired food was a vine growing on the sapling. Diospyros trees, in particular, suffered from the activity of gorillas, as many were small trees incapable of supporting an adult gorilla's weight; branches were pulled towards the ground and snapped.

2. Food Processing

a) Structural Plant Parts.

Aframomum - the stem was anchored by the teeth and pulled with the hands to split the tough outer sheath and expose the inner pith, which was ingested (Figure 4.4).

Anchomanes difformis - the stem of this fleshy, herbaceous plant was peeled and the

inner tissues consumed. Leaves were stripped from the petioles with the teeth.

Anisotes macrophyllus - the stems were bent and broken, but not detached from the roots; leaves were bitten in half or drawn through the teeth, stripping away the tissues and leaving behind the midribs.

Chlorophora excelsa - branches were broken off and completely stripped of bark, bunches of terminal leaves often remained attached to dropped branches. Some leafy twigs were left draped over branches.

Dialium sp. - only the tips of young leaves were swallowed, leaf bases and petioles were spat out in little heaps.

Eremospatha cabrae - leaves were pulled through the teeth, leaving the ribs behind (Figure 4.5).

Haumania and Megaphrynium - the bases of young leaves were bitten off (Figure 4.6) and developing leaves were removed from inside stems or shoots.

Marantochloa and Halopegia - 10-15 cm portion of the tender, pink stem-bases were eaten, and the rest was discarded.

Milletia versicolor - saplings were completely stripped of bark, except for the base of the trunk. Twigs of an unidentified shrub were eaten in the same manner (Figure 4.7).

b) Fruits.

Fruits were treated in differing ways; usually they were dealt with individually and many succulent fruits were swallowed whole. Seeds of only 5 types were selectively extracted from fruit by gorillas, rather than swallowed passively with pulp (Apocynaceae spp., Detarium macrocarpum, Haumania sp., Parkia bicolor and Pentadesma butyracea). The seeds or skins of particular fruits were sometimes spat out, including those of Hexalobus crispiflora, Megaphrynium gabonense and Pseudospondias longifolia. Some large seeds were rarely (Klainedoxa gabonensis) or never (Irvingia grandifolia, Saccoglottis gabonensis) swallowed. Small piles of clean seeds or 'stones', skin, and rejected fruits were left at feeding-sites. For reasons unknown, a few seeds of 5 species were crunched up, but most passed though the digestive tract unharmed. Although the increased load of seeds impairs the benefits of pulp (Herrera, 1981), the cost of having about half of the gut volume taken up by seeds is generally outweighed by the increase in

handling time necessary to extract seeds from pulp (Milton, 1984). Undigested whole fruits were excreted after some periods of intense feeding on Celtis tessmannii, Cissus sp. and Uapaca guineensis amongst others, probably because they were not properly masticated before swallowing. Some examples of ways in which fruits were manipulated are given below:

Dialium sp. - the brittle, flattened seed cases were bitten in half and processed rapidly, 20-30 per minute, judging from the rate of popping sounds. These noises were loud enough for us to locate previously undetected apes. Seeds and pulp were swallowed and the cases spat out.

Detarium macrocarpum - this large fruit with dense green pulp encased a hard discoid seed, 6-7 cm in diameter. The kernel is procured by chimpanzees in the Ivory Coast using stone hammers (Whitesides, 1985). Gorillas are not known to use tools in the wild, and depended on the strength of their jaw musculature to break open the seeds. It seemed that Detarium could be processed by adult male gorillas only. The pulp was discarded and once was accompanied by crushed Marantaceae leaves, smeared with pulp, on which the gorilla had apparently wiped his hands. One lone male ate 7 kernels at a single sitting.

Duboscia macrocarpa - this species was a major food-item, though seemingly unpalatable. The 4-6 cm ribbed fruit had a brown, velveteen skin, and the 'pulp' had the texture of a scrubbing brush (Figure 4.8). The seeds resembled those of an apple, and the remains of a meal were left like apple cores. Many fruits were bitten into, but left on the ground.

Myrianthus arboreus - these large, yellow, composite fruits had a thick skin, similar to that of a pineapple. They consisted of about 70 segments each containing a single seed encased in sugary pulp. Gorillas broke pieces off fruits, extracted the seeds and pulp, then discarded the empty segments together with some sucked and spat-out seeds.

Pentadesma butyracea - the size of a small melon, these were the largest soft fruits known to occur at Lope. The pulp was orangey-pink and sticky with latex. Whole fruits were rarely consumed, and the 3 cm seeds were sometimes cleaned and discarded. One adult female was observed to eat 4 fruits in 2 minutes, spitting out only one seed.

The above descriptions illustrate the dexterity involved in food preparation. Other methods have been described in detail by Schaller (1963), Goodall (1974), and Fossey and Harcourt (1977), and the processing of food-items by gorillas seems to be similar throughout their range.

c) Invertebrates.

Weaver ants were deliberately consumed: crushed leaves with a few dead ants stuck to them were found on gorilla trail. The presence of wings, and queens' heads in dung, as well as those of the worker forms, implied that whole nest contents had been swallowed, and not just stray ants on vegetation.

The black ants consumed have not been identified. Their numbers in the dung suggested that ingestion had been intentional. Once gorillas walked 50 m along an open road into the savanna and entered a clump of Nauclea latifolia shrubs covered in ants. The trail then changed direction and headed back towards the forest. Split-stems of Psidium sp. which had housed the black ants were also found on gorillas' trail.

D. VARIATION IN THE DIET

1. Diversity

a) Overall.

The Shannon-Weaver index of diversity (Pielou, 1966, see Chapter 3) was calculated for fruits only, as the number of species of leaves and stems consumed could not be determined. The index gave a measure of variety in the diet and of how evenly species were used, and was calculated to be 2.7 for diversity of the fruit diet, 2.9 for the pulp consumed. Diversity of species-use was 3.2. Even though structural parts were excluded, these values exceeded those obtained by Watts (1984) for mountain gorillas, whose diversity of species-use was 1.8, and dietetic diversity was 2.2 (for individual groups). However, Watts (1983:151) thought it likely that mountain gorillas have the least diverse diet among the apes. At Lope 5 species made up half of the total fruit diet; 20 species (35.7%) formed 96% RPC. This broad diet was appropriate to the heterogeneous habitat, where few species were abundant and dietary overlap within the frugivorous community

was extensive (cf. Emmons et al, 1983; Gautier-Hion et al, 1985b). Interannual variation in the diet was high, as shown by the following monthly scores.

b) Monthly Variation.

Variation between months was significant at the 0.001 level for all parameters measured in the dung, that is, stem-fibre (F = 8.7), leaf fragments (F = 38.8), RFC (F = 21.6), RPC (F = 28.6), relative seed consumption (F = 14.2), ants (F = 3.3),and the number of fruit species (F = 14.3). Consumption of ants was non-normally distributed and was therefore subjected to a Kruskal-Wallis 1-way ANOVA, which also produced a significant result (χ^2 corrected for ties = 54.0, $p<.01$). Correlation values were calculated between all food-types (Table 4.3).

The species overlap between adjacent months was substantial (mean = 50.6% species shared, Table 4.4). On average 14 fruit species were eaten each month (by more than one group) (R = 7-20, see Figure 4.9), however, the number of species recorded was correlated with the number of dung samples collected each month ($r(17)=.78$, $p<.001$).

c) Daily Diversity.

The average number of foods per trail was 3.3 species (R = 1-9), and 3.7 types (R = 1-11). The number of items in dung samples averaged 5.4 (R = 2-12). However, this number under-represented structural parts as, for instance, all species of leaves were recorded by a single category. To avoid unequivocal representation of each food class, some analyses were limited to the more comprehensive data on fruit diet. So, from here on 'items' refers to fruit only, and was equivalent to species, as parts eaten simultaneously were recorded as a single type (Figure 4.9). The mean number of fruit items in dung samples was 3.0 (R = 0-8). (N.B. this represents <24 hr, but for convenience was termed 'daily'). 'Items' was positively correlated with the above measures of fruit consumption (Table 4.3). This suggests that even if a preferred species was abundant, the gorillas sought a variety of fruits each day. Moving from one food source to another, rather than depleting a particular source, would have helped to achieve nutritional balance (e.g. Garber, 1987).

Table 4.3 Pearson Correlation Coefficients For Food-Types Recorded in the Dung of Gorillas at Lope

	fibRPC	RPC	fibre	glfs	shrubRFC	items	ants	fibRFC
RFC	.1328 (629) P= .001	.8625 (629) P= .000	-.2452 (629) P= .000	-.3885 (629) P= .000	-.6478 (16) P= .007	.3726 (629) P= .000	-.1143 (629) P= .004	.1328 (629) P= .001
fibRPC		.0110 (629) P= .783	.1637 (629) P= .000	.1614 (629) P= .000	.0532 (16) P= .845	.1006 (629) P= .012	-.0224 (629) P= .576	1.0000 (629) P= .
RPC			-.2478 (629) P= .000	-.3373 (629) P= .000	-.6496 (16) P= .006	.2876 (629) P= .000	-.0829 (629) P= .038	.0110 (629) P= .783
fibre				.2689 (629) P= .000	.4677 (16) P= .068	-.2015 (629) P= .000	.0183 (629) P= .647	.1637 (629) P= .000
glfs					.3602 (16) P= .171	-.2784 (629) P= .000	.1328 (629) P= .001	.1614 (629) P= .000
shrubRFC						-.5380 (16) P= .032	-.4289 (16) P= .097	.0852 (16) P= .754
items							.0057 (629) P= .887	.1006 (629) P= .012

UNITS OF CORRELATION: 629 = individual dung samples; 16 = monthly averages

KEY: RFC = relative fruit consumption, RPC = relative pulp consumption, ants = weaver ants, fibRPC = RPC of fibrous fruits, fibRFC = RFC of fibrous fruits, glfs = leaf fragments, items = no. of fruit species, fibre = stem-fibre, shrubRFC = RFC of shrub & vine fruits,

Table 4.4 Overlap in the Fruit Diet of Gorillas at Lope Between Neighbouring Months

MONTH	NUMBER OF SPECIES	SPECIES OVERLAP	% SPECIES OVERLAP
1984:			
January	13		
February	14	6	44.5
March	14	6	42.9
April	7	6	64.3
May	15	4	41.9
June	11	7	55.2
July	9	6	60.6
August	13	5	47.0
September	13	7	53.8
October	20	10	63.5
November	17	11	59.9
December	14	7	45.6
1985:			
January	20	9	54.6
February	16	12	67.5
March	14	6	40.2
April	16	10	67.0
May	11	10	76.7

Mean overlap = 50.6%, range = 40.2 to 76.6%
(overlaps calculated with previous month)

Figure 4.9 Diversity of Fruit Species Eaten by Gorillas at Lope

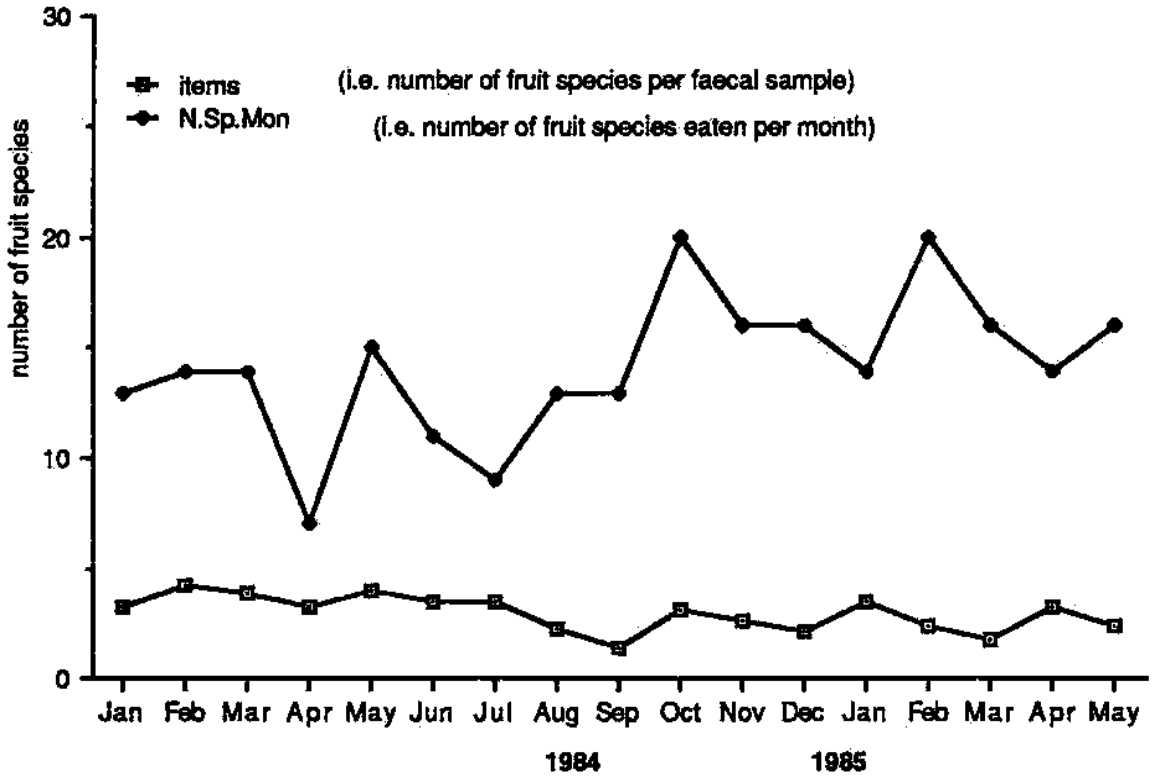
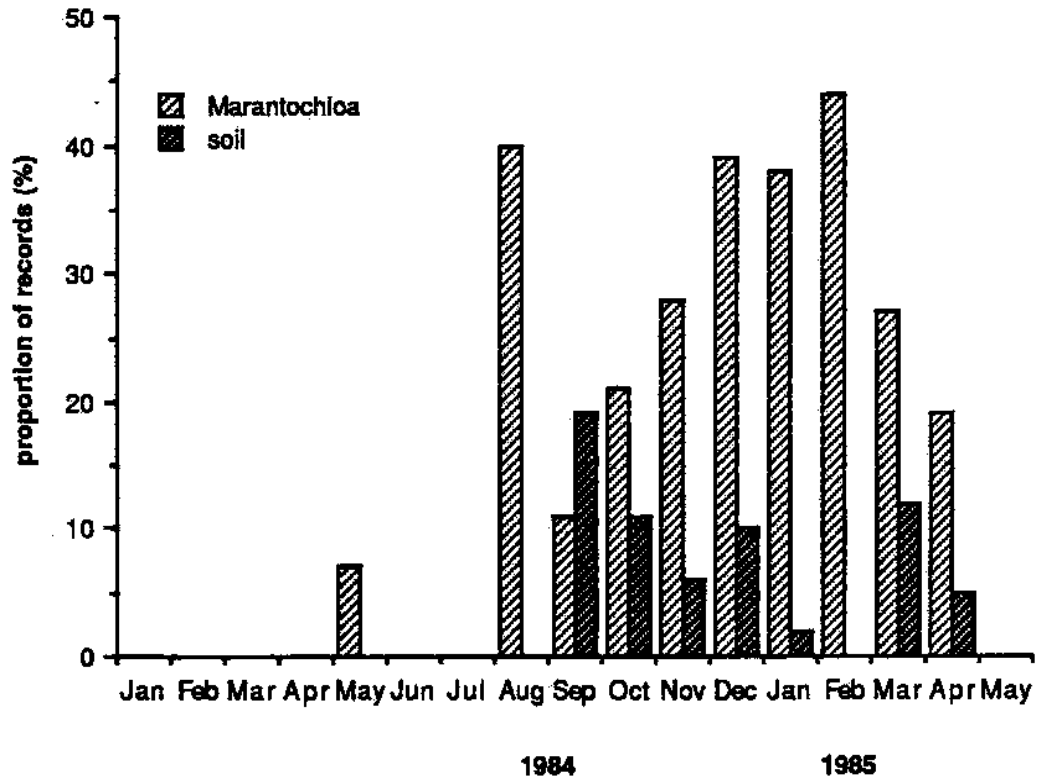


Figure 4. 10 Monthly Variation in Consumption of Marantochloa and Soil



2. Structural Plant Parts

a) Stems.

Foraging in streams was sporadic: from May 1984 to April 1985, 64 occurrences were recorded, involving at least 7 groups of gorillas (Figure 4.10). A high incidence of feeding on Marantochloa stem-bases coincided with consumption of leaves ($r(16)=.7370$, $p=.001$), and fibrous fruits ($r(16)=.6855$, $p=.003$), but did not relate to total stem-fibre consumption, or fruit availablity. Thus aquatic herbs were substitutes for neither fruit, nor Aframomum pith, but were an additional food source.

Aframomum was eaten throughout the year, and was consistently abundant, although changes may have occurred in stem quality or in the proportion of tender new shoots, which we did not detect. Traces of feeding on Aframomum were denser and more conspicuous when fruit availablity (FAI) was low, especially during the major dry season, suggesting that more Aframomum was eaten (Figure 4.11). Conversely less stem-fibre was recorded in the dung when large quantities of fruit were eaten, as shown by a significant negative correlation (Table 4.3).

The extent to which variation in the amount of stem-fibre scored in the dung would have reflected actual intake merits further attention. The minimum monthly value for fruit consumption (RPC) and maximum value for stem-fibre consumption both occurred in August 1984. Also, less fibre was present when seed volumes in the dung were high, as shown by a negative correlation ($r(629)=-.1932$, $p<.001$). Dung may have been eliminated more often, to get rid of bulky seeds in the gut, if the total volume of food eaten had increased as more fruit was ingested. Thus, even if stem-fibre intake had remained constant, fibre would have become a relatively smaller portion of each sample. Fibre was judged in relation to the bulk of a sample and the accompanying volume of seeds, so to avoid the influence of seed volumes, a measure of the fruit fraction *not* present in the faeces should be considered: RPC values (pulp consumed) represented *digested* fruit. A significant negative correlation between RPC and fibre values also suggested that stem-fibre intake was reduced when fruit consumption was high (Table 4.3).

b) Leaves.

The proportion of leaves in the diet was more variable than that of stem-fibre, but

Figure 4.11 Monthly Variation in the Relative Abundance of Some Food-Types in Gorillas' Dung

abundance ratings: 0 = none, 1 = rare, 2 = few, 3 = common, 4 = abundant

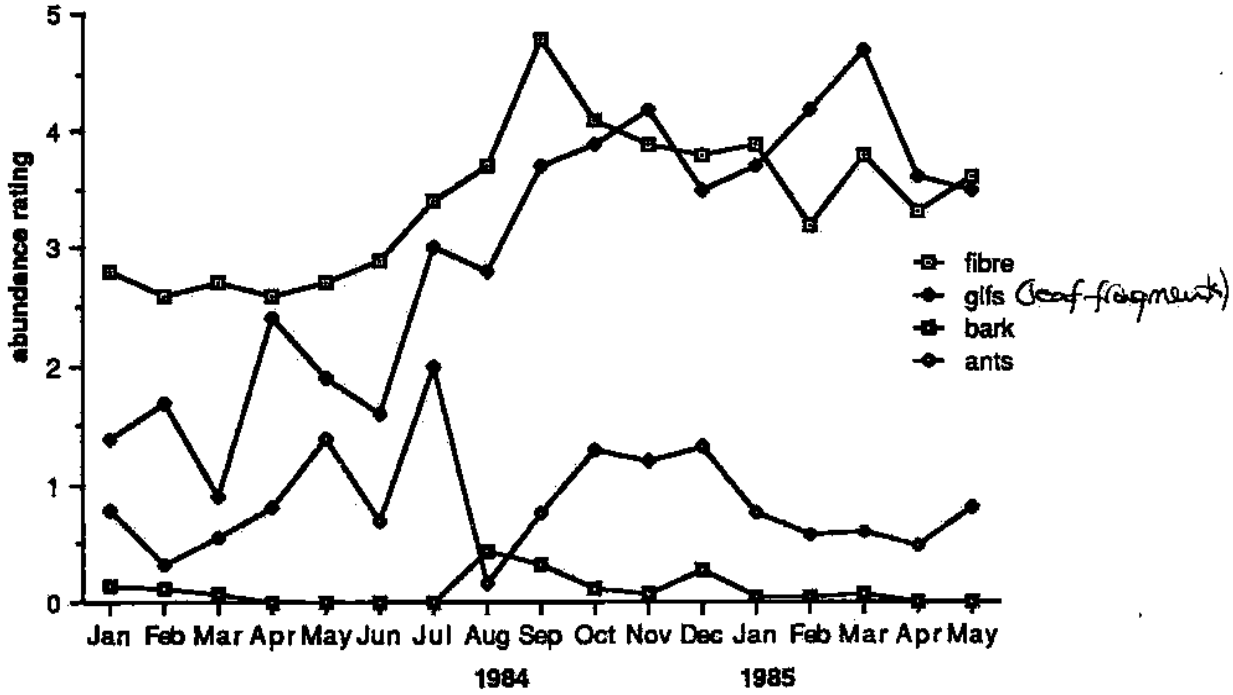
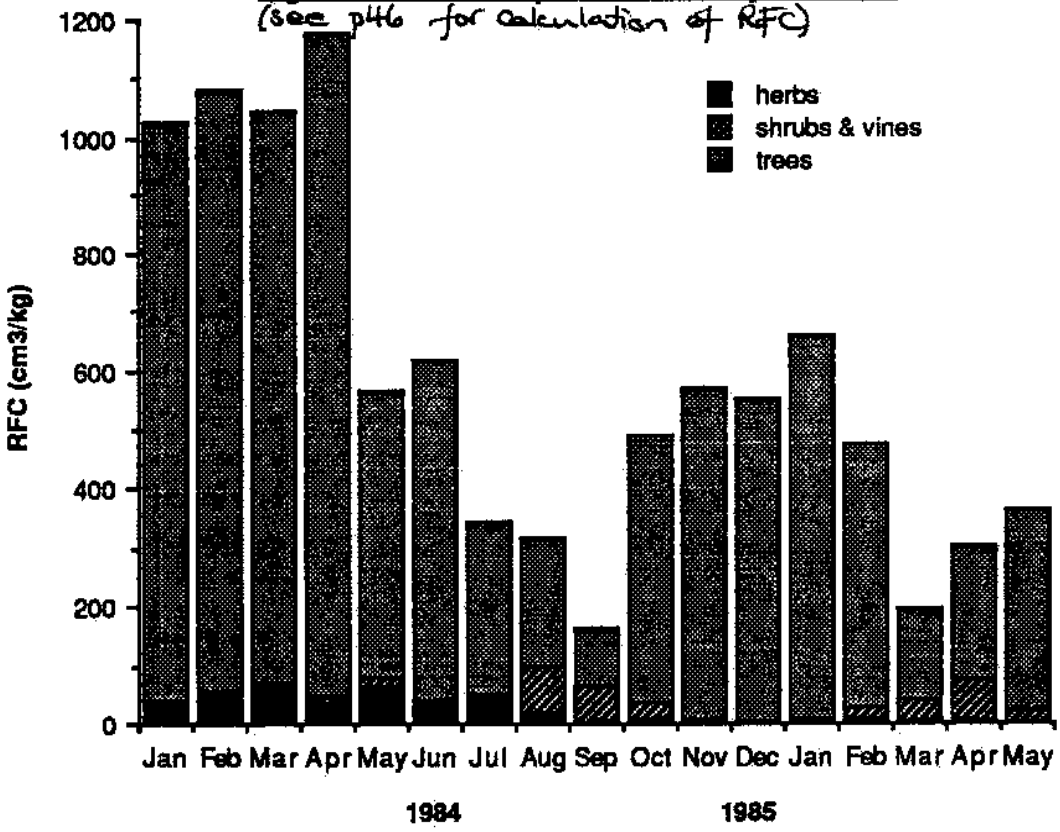


Figure 4.12 Consumption of Fruits by Life Form

(see p46 for calculation of RFC)



some were almost always eaten, probably for their protein content. Chimpanzees at M'passa obtained most of their dietary protein from leaves (Hladik & Viroben, 1974). Protein levels are about 2.5 times higher in Leguminosae leaves (Hladik, 1978), than in mature leaves in general, and leaves from 3 species of legumes were found in the dung of gorillas at Lope: Crytosepalum staudtii, Pentaclethra eetveldeana, and P.macrophylla.

Fewest leaf fragments were recorded in the dung during early 1984 (Figure 4.11). The peaks of consumption, in November 1984 and February-March 1985, corresponded with maximal production of new leaves (see Chapter 3). Leaf ingestion was also significantly negatively correlated with measures of fruit consumption (Table 4.3), however no significant correlations were found between leaf ingestion and the phenology of new leaves or total leaf cover on trees (Table 4.5), or Marantaceae leaf production ($r(10)=.1688$, $p=.641$).

c) Bark.

Goodall (1977) found that mountain gorillas selected bark even when foliage was available, and he suggested that bark was eaten for the physical action in the gut. At Lope virtually no bark was recorded in the dung during the first 6 months of 1984, when fruit consumption was very high (Figure 4.11). Bark ingestion peaked during August and September, when fruit values were minimal, but no significant correlations were apparent. As mentioned above, Chlorophora excelsa was an important source of bark, and evidence from trails was found throughout early 1985, mostly when fruit was scarce.

3. Fruit

Two annual peaks of fruit consumption occurred: one in the short dry season, and a smaller one in the major rainy season. Fruit eating was minimal during the long dry season. Striking differences were found between 1984 and 1985, due to the failure of, or reduction in, many fruit crops. Figures 4.12 and 4.13 show the RFC and RPC values for each month. There was a 7-fold variation in fruit ingestion between months related to the availabilty of edible fruits. RFC and RPC were positively correlated with FAI, but not with the median phenology scores for all trees combined (see Table 4.5). Tree-fruits dominated the general pattern of intake (Figure 4.12).

Figure 4.13 Relative Consumption of Succulent and Fibrous Fruit
(see p46 for calculation of RFCs)

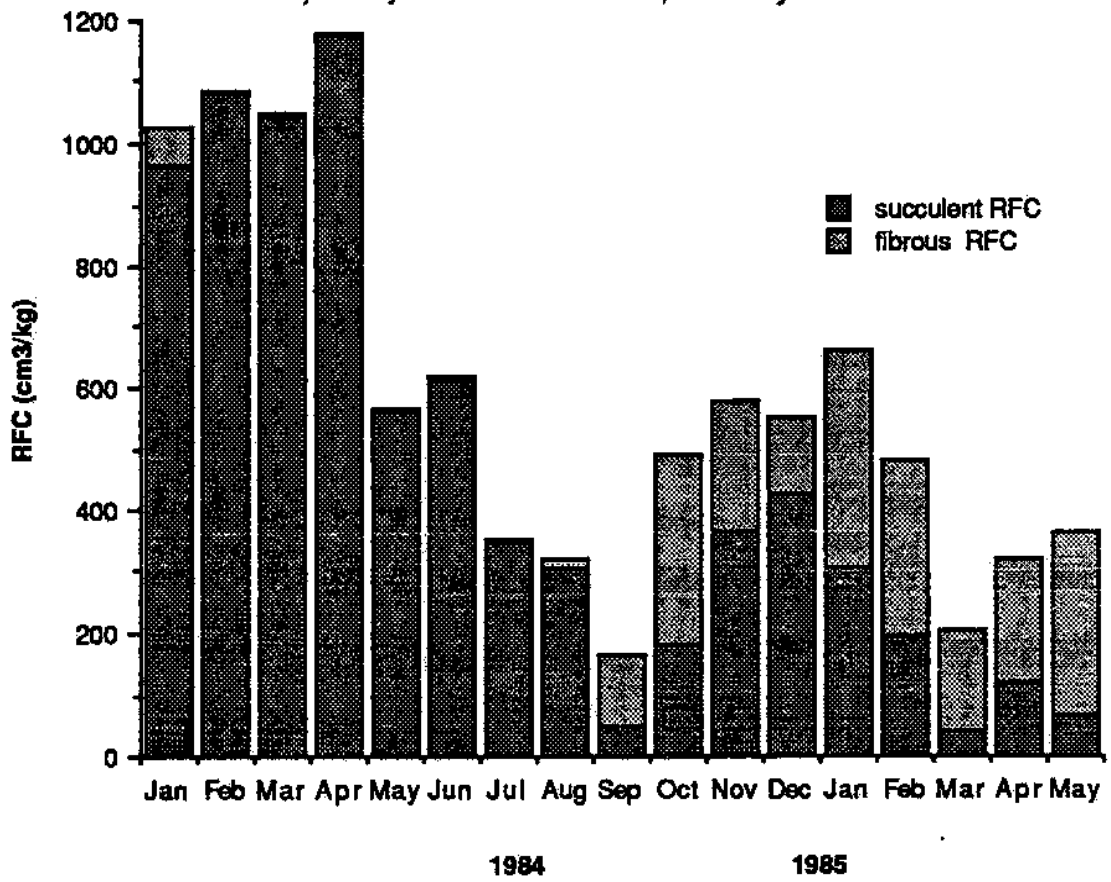
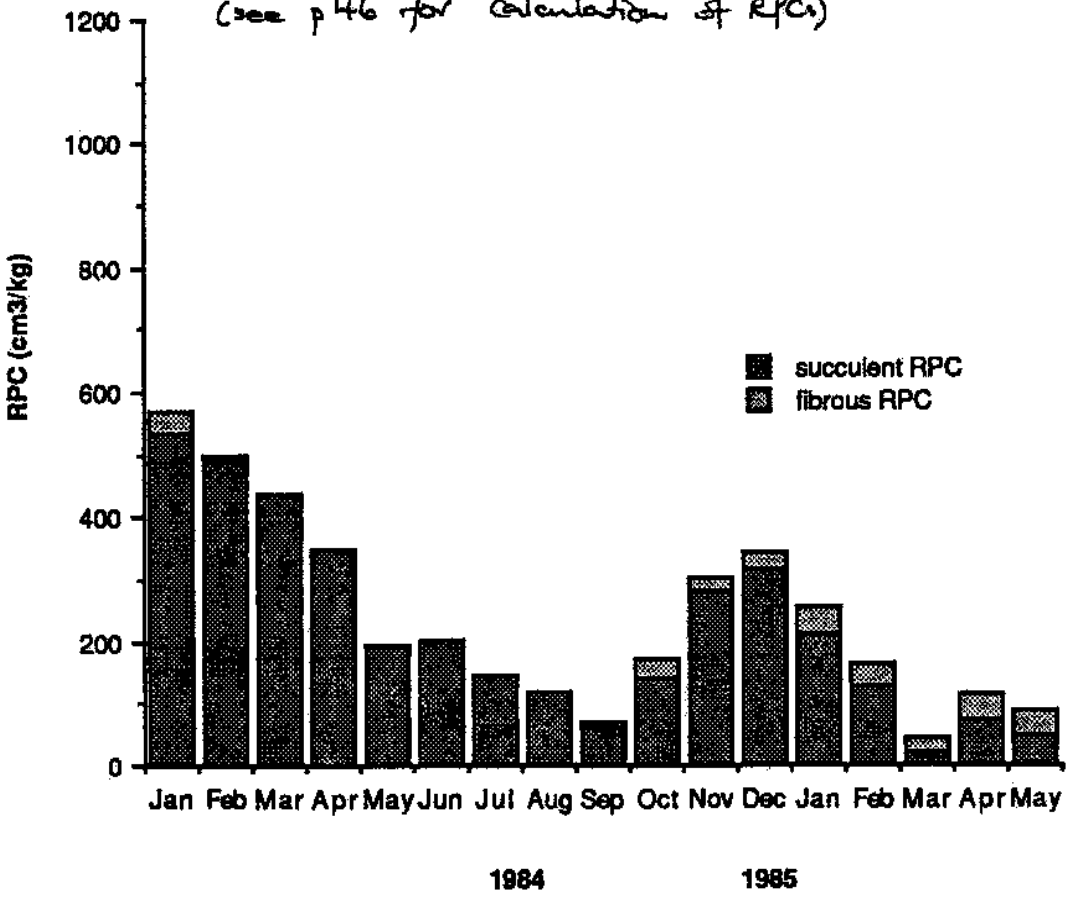


Figure 4.14 Relative Consumption of Succulent and Fibrous Pulp
(see p46 for calculation of RPCs)



a) Herbaceous Fruits.

The fruits of Aframomum were eaten mostly in the first 7 months of the study. The decrease in consumption which followed was due to lack of availability. Aframomum fruits were eaten most during a period when RFC and RPC values were maximal, and were therefore a preferred fruit source (Figure 4.12).

b) Shrubs & Vines.

Consumption of fruits from shrubs and vines was high during 4 months (August and September 1984, March and April 1985), reaching a maximum of 77.6 cm^3 in August, when overall fruit availability was low (Figure 4.12). Consumption was negatively correlated with RFC, RPC and FAI (Tables 4.3 and 4.5). The 10 species eaten were used as alternative fruit sources during periods of low production by food-trees, although data on availability are needed to make inferences about selectivity. Elsewhere understorey "treelets" often produce small aseasonal crops (Leighton & Leighton, 1983).

c) Fruit Quality.

Sugary fruits were a major part of the diet. Interannual variability was exemplified by March, April and May: in this period of 1984, 100% of the RPC was succulent fruit; in the same months of 1985 the succulent portion was reduced to 35%, 57% and 53% of the RPC respectively. Virtually no fibrous fruits were eaten for the first 8 months of the study, when succulent fruit consumption was very high, but thereafter Duboscia and Klainedoxa were eaten in large quantities, despite their low nutritional values. RPC values fell below 60% of succulent fruit during only 4 months (September 1984, March and May 1985). During the same period fibrous fruit formed more than 25% fruit diet. Fibrous fruits contributed largely to RFC values (21.4%), but as a considerable fraction was undigestible they formed only 7.7% of the RPC (Figures 4.13 and 4.14). Although overall fruit consumption was negatively correlated with ingestion of leaves, fibrous fruits were positively correlated with leaves (Table 4.3), and there was a tendency for succulent and fibrous fruit to be inversely related, although not significantly ($F=-.4414$, $p=.076$). This suggested that more fibrous fruits were eaten when less succulent fruit was available. Assuming that fibrous fruits had low nutritional values, and that other fruit types were generally insignificant, succulent fruit intake may be taken as an indicator

of the gorillas' dietary quality, in which case the poorest months were September, and March-May 1985. It should be noted that Pentadesma butyracea accounted for 55-65% RPC in January and February 1985. This fruit was placed in the succulent fruit category, although preliminary analyses indicated relatively high fibre and low sugar contents. Further analyses are needed to confirm the nutrient composition.

4. Invertebrates

At Lope the frequency of Oecophylla longinoda ingestion peaked from October to December, when over 47% of the dung contained ants' remains (Figure 4.11). Consumption during February and May was lower, but no patterns were discernable in early 1984. (The high scores for April and July are probably anomalous, caused by small sample sizes for those months). Feeding on ants was positively correlated with feeding on leaves, and negatively correlated with fruit consumption (Table 4.3). Baldwin (1979:127) proposed that consumption of weaver ants by chimpanzees in Tanzania (Goodall, 1968:187) and Senegal varied with seasonal reproduction of the ants. The composition of weaver-ant social units is not constant (Ledoux, 1950) and at Lope the number of larvae in nests may have varied seasonally, but no data were available to investigate this.

5. Age-Class Differences

Sex and age-classes were judged from dung diameters (see Chapter 2). When the diet included a lot of fibre the lobes were well formed, but when more fruits were eaten, especially fruits with large seeds, the dung was soft or contained little matrix, and did not retain its shape. Thus few age-classes were ascertained during some months, and analyses were restricted to the latter 6 months of the study with the largest samples (N = 221, subset = 193). The mean weights of the categories used in statistical tests were:

(i) silverback males:	707 g,	sd = 577
(ii) adult females and sub-adults:	316 g,	sd = 249
(iii) juveniles and infants:	208 g,	sd = 226

The differences between these means were significant ($F=31.3$, $p<.001$), but the overlap

between them was too great for weight to be used as a criterion to determine age-classes.

Gorillas of all ages were observed feeding arboreally, and it seemed that they consumed relatively equivalent amounts of fruit. Smaller animals might have been expected to obtain a larger proportion of fruit by climbing, as more trees could support their body weight, but the range between RFC values for each class was only 1.5%. Differences between age-sex classes were not significant, although large animals consumed more fibrous fruit, particularly Klainedoxa gabonensis, than did juveniles and infants. Also strength seemed to determine the ability to feed on Detarium macrocarpum seeds, which were eaten by silverbacks only. Fossey and Harcourt (1977) reported that immature mountain gorillas spent 18.2% of their feeding time in trees, where they also often played, but that adults climbed only when fruit was available (3.6% time). Watts (1984) found that individual selection by the mountain subspecies accounted for most variance in the diet, and that this was related to the strength required to uproot particular items: younger animals experienced some processing difficulties, but no consistent age-class differences were found.

6. Group Differences

Three groups were compared over 7 months when adequate data were recorded (N = 259 dung samples). Tree diversity and density were not the same in each group's home range, and their diets differed accordingly (although it should be noted that home ranges were not exclusive, see Chapter 6). Significant differences were found in RPC values and seed volumes, as pulp:seed ratios varied between species. These differences may have been caused by restraints of the gorillas' digestive physiology: if they maximised fruit intake, but consumption was constrained by gut capacity and digestion rates, the 'waste' volume occupied by indigestible seeds could not have been compensated for by eating even more fruit.

Group differences were typified by the use of foods on the savannas: the grasslands offered little food, other than Antidesma vogelianum and Psidium sp. (wild guava). These shrubs grew in the transitional vegetation at the forest's edge, and produced small fruits, which gorillas living close to the savanna borders fed on. 'Savanna fruits'

composed 2.3% of the RFC, but most were consumed by Group 5:

Group 3	4.4 cm^3,	0.7%	RFC
" 4	1.2 cm^3,	0.3%	"
" 5	36.8 cm^3,	7.6%	"

Group 5 (St. Exupery) inhabited the main forest block, but the core of its home range cut across the savanna. Its members ate no Scytopetalum klaineanum, which occurred only on ridge tops in the forest, no Porterandia cladantha, relatively small quantities of Duboscia macrocarpa and Klainedoxa gabonensis, but large quantities of Psidium sp. at the savanna edges and Uapaca guineensis in gallery forests. The stem-fibre and leaf scores for this group were the lowest. Savanna foods may have provided alternative sources of fruit, thus reducing dependance on other food-types.

Group 4's (Victor Hugo) range was furthest into the forest block. The members of this group ate large amounts of Klainedoxa, Porterandia and Scytopetalum fruits, but no Antidesma or Psychotria shrubs.'Items' was lowest for this group, suggesting that the daily fruit diet may have been less diverse when access to 'savanna fruits', and hence the range of species available, was more limited. Group 4 also had the highest scores for bark and ants, which may have provided alternative food-types if fewer species of fruit were available.

Group 3 (Monte Cristo) was intermediate, overlapping with both Groups 4 and 5. No striking dietary differences were found, although consumption of Pentadesma butyracea and Nauclea didderichi was high, while that of Scytopetalum was low.

Groups of mountain gorillas showed basically similar patterns of food choice, and differences were caused by variation in food density (Fossey & Harcourt, 1977), and contrasts in the vegetation of their respective home ranges (Watts, 1984). A similar explanation seemed to account for the minor differences found between groups at Lope.

E. SELECTIVITY

1. Reasons For Selectivity

Dietary demands are set by metabolic rates, but numerous other factors lead to

compromises in food selection by primates (e.g. Milton, 1981a; Demment, 1983). The constraints imposed on food choice include:

a) properties of the food (i) availability, (ii) accessibility, (iii) palatability, (iv) weight, (v) profit margin, (vi) nutritional quality and changes therein (e.g. Goodall, 1974);

b) physiological characteristics of the consumer (i) nutritional requirement, and (ii) digestive capacity and retention time (e.g. Milton, 1979);

c) ecological factors such as: (i) competition, and (ii) number and availablity of optional foods (e.g. Baranga, 1986).

Selection and preferences are not the same: selection is independent of other food-types; a preferred food is one chosen when other items are simultaneously available. Watts (1984) demonstrated selection by Gorilla gorilla beringei. preferences for certain foods, and the existence of a negative relationship between these two factors. Casimir (1975) described mountain gorillas' choice of diet as "protein-orientated" and noted a strong preference for bamboo, which was eaten almost to the exclusion of other food-items at the height of the bamboo's growth season.

Lowland gorillas were selective at several levels, choosing between species, parts, and individual specimens. They ate items from relatively few of the wide range of foods available, for example, parts of only 31.9% of the tree species recorded on transects. Entire plants were never eaten. Instead specific parts were removed from each, such as the bases of developing Haumania leaves, the inner pith of Aframomum, and the bases of Marantochloa stems. Differences in chemical composition between plant parts (such as ripe and unripe fruit, new and mature leaves), and primates' preferences in relation to these factors have been well documented (e.g. Herrera, 1982; Hladik, 1978; Milton, 1979; Oates et al, 1977). For example, condensed tannins are detoxified during ripening, increasing the palatability and digestibility of fruits. The gorillas at Lope rejected both under- and over-ripe fruits, while some ripe fruits were only partially eaten.

2. Structural Plant Parts

At Lope Aframomum and Haumania were the gorillas' staple foods (permanent food

sources), as they were abundant, easily accessible (foraging did not require climbing), and the herb layer is comparatively less toxic than the canopy (Hladik, 1981; Waterman, 1984). Young tissues such as new shoots were often selected, as differentiating cells are generally rich in protein and carbohydrate (see Nishida, 1976). Phytochemical comparisons of 4 species of herbaceous plants from Lope revealed that fibre was generally 25% lower in parts eaten, than in parts discarded, while protein content was up to 50% higher (Rogers, in prep.). Succulent stem-bases, such as those of Marantochloa, may have been more digestible due to their lower fibre content. Marantochloa may also have been high in sodium and other minerals, like the swamp plants eaten by guereza monkeys, Colobus guezera (Oates, 1978).

Leaves were not picked at random, but carefully removed from particular plants. The levels of secondary compounds in leaves are known to vary between species, and some primates are able to discriminate between individual trees within a species (Glander, 1981).

Bark was eaten as an emergency food during periods of fruit scarcity by chimpanzees in Tanzania (Nishida, 1976), and it fulfilled a similar function for orang-utans (MacKinnon, 1974; Galdikas, 1979). Gorillas at Lope fed on bark mostly when fruit consumption was low, but only small quantities were ingested, and this trend was not significant.

3. Invertebrates

Two hypotheses have been advanced to explain why primates eat insects:

(i) that ingestion is inadvertant, and

(ii) that invertebrates form an essential part of the protein diet.

The thousands of invertebrates inadvertantly ingested per day by mountain gorillas amounted to less than 2g, and Harcourt and Harcourt (1984) did not consider this animal matter to be necessary from a nutritional viewpoint, although there has been doubt that a purely vegetarian diet is tenable for gorillas (Brambell, 1972; T-W-Fiennes, 1972). Casimir (1975) and Goodall (1977) estimated that plant matter supplied eastern lowland gorillas with adequate amounts of protein and gross energy.

Nishida and Hiraiwa (1982) suggested that chimpanzees at Mahale ate ants for their spicy taste, asserting that they contained trivial quantities of protein. However according to Hladik (1977), the grubs of Oecophylla have a high amino acid content (71.5%) in a readily digestible form, which complements the protein obtained from leaves (Hladik & Viroben, 1974). The similarity in the proportions of gorillas' dung which contained insects' remains at Lope and Belinga (31.1% and 30.5%) makes inadvertant ingestion seem an unlikely explanation. Termite-eating by chimpanzees is nutritionally orientated (e.g. Redford, 1987), and I propose that weaver ants and termites have the same role in the gorillas' diet in Gabon.

4. Earth

There have been 2 main interpretations of the benefits of soil consumption: (i) that animals eat earth to obtain minerals; and (ii) that fine soils adsorb some of the secondary compounds present in leaves, while the mineral content is of negligible importance. Soils have been analysed from many sites, and sodium, in particular, has been measured in higher concentrations at salt-licks than in the surrounding areas (e.g. Schaller, 1963:371; Stark, 1986). Some studies have denied any apparent physiological benefits of geophagy (Stark, 1986; Ganzhorn, 1987), but salt-licking by chimpanzees at Gombe was associated with changes in body weight, suggesting that salt requirement increased with metabolic stress (Wrangham, 1977). Hladik and Gueguen (1974) found that the sodium content of soils seemed insignificant compared to that of some food plants, especially Hypselodelphis shoots. This view point was reiterated by Harrison and Hladik (1986), as geophagy by Colobus satanus coincided with peaks of leaf ingestion. At Lope earth was recorded in over 10% of dung during 3 months (September, October, December, see Figure 4.10), which correlated with a peak in leaf consumption by gorillas ($r(629)=.1232$, $p=.002$). However conclusions drawn from these preliminary results should only be tentative.

5. Selection Of Fruit

The gorillas' preference for fruit was demonstrated by the following trends:

(i) fruit was selected when vegetative plant parts were simultaneously available in large quantities;

(ii) when fruit formed a high proportion of the diet fewer leaves and stem-fibre were consumed;

(iii) stem-fibre and leaf consumption was influenced more by the availability of fruit, than by their own abundance.

Gorillas preferred particular species of fruit, as shown by the lack of a correlation between fruit consumption and the median phenology scores for the community, whereas a positive correlation was produced with the more selective measure of fruit availablity, FAI (Table 4.5). Some abundant types of fruit were avoided, notably 10 species of Caesalpiniaceae and Mimosaceae (although their new leaves were consumed). The seeds of these Legumes were wind-dispersed, or explosive, and so they were not embedded in pulp. As mentioned above, many seeds contain high concentrations of secondary compounds, and seed-eating necessitates gut specialisations which gorillas do not have (Andrews & Aiello, 1984; Chivers & Hladik, 1980).

Several fruit species which were relatively unimportant to gorillas formed a major part of the chimpanzees' diet, including 2 members of the Burseraceae, Canarium schweinfurthii and Dacryodes buttneri, the oil palm Elaeis guineensis, Polyalthia suaveolens and Staudtia gabonensis. These species all contain high concentrations of lipid (e.g. Leighton & Leighton, 1983). The Burseraceae also produce resins (Saint Aubin, 1963), although gorillas ate one species, Santiria trimera, in large quantities. They also ate one arilled fruit, Pycnanthus angolensis, in small quantities. There was no obvious explanation for the choice differences between gorillas and chimpanzees, but selection may have been influenced by discrete features, such as vitamin or mineral content of fruits.

The gorillas' food preferences were not constant. 'Non-preferred' fruits, such as Diospyros polystemon, Hexalobus crispiflora, Myrianthus arboreus and Pseudospondias microcarpa, were ignored during times of fruit affluence, but were eaten

Table 4.5 Pearson Correlation Coefficients For Measures of Phenology and Food-Types Recorded in the Dung of Gorillas at Lope

	RFC	RPC	fibre	glfs	shrubRFC	items	fibRFC
FAI	.7856 (10) P= .007	.9360 (10) P= .000	-.0725 (10) P= .842	.2215 (10) P= .539	-.7989 (10) P= .006	.2536 (10) P= .480	.2189 (10) P= .544
phenolFR	.2951 (10) P= .408	.0899 (10) P= .805	.1890 (10) P= .601	-.5250 (10) P= .119	-.0913 (10) P= .802	.5396 (10) P= .107	.3843 (10) P= .273
phenolNL	.7190 (10) P= .019	.7384 (10) P= .015	-.4664 (10) P= .174	.3648 (10) P= .300	-.8032 (10) P= .005	.3342 (10) P= .345	.4546 (10) P= .187
phenolML	.1407 (10) P= .698	.1031 (10) P= .777	.4284 (10) P= .217	.5346 (10) P= .111	-.5366 (10) P= .110	-.1835 (10) P= .612	.4483 (10) P= .194

KEY: RFC = relative fruit consumption, RPC = relative pulp consumption, fibRFC = RFC of fibrous fruits, shrubRFC = RFC of shrub & vine fruits, items = no. of fruit species, fibre = stem-fibre, glfs = leaf fragments, FAI = food availability index, phenolFR = fruiting scores of community, phenolNL = new-leaf production, phenolML = total leaf cover of community

UNIT OF CORRELATION = months

when favoured fruits were scarce. This subjective assessment was made during the early stages of the study before phenological data were available, and requires further investigation. Fruits which were eaten in small quantities only may have contained tannins which could not be tolerated at higher levels (see Janzen, 1978). Secondary compounds in Pavetta puberula may explain why bunches of fruit were ignored when gorillas stripped leaves from fruit-bearing shrubs. At Kahuzi-Biega eastern lowland gorillas avoided parts of 3 food-plants, including fruits, which contained toxins (Casimir, 1975).

6. Fibrous Fruits

The 'less preferred' fibrous fruits, Duboscia macrocarpa and Klainedoxa gabonensis, deserve further consideration. Detarium macrocarpum, Duboscia macrocarpa, Panda oleosa, and Pentadesma butyracea were not listed as primate foods by Gautier-Hion et al (1985b), and fibrous fruits were avoided by Cercopithecus monkeys at M'passa (Sourd & Gautier-Hion, 1986). Also, Calvert (1985) remarked that the woody fruits eaten by gorillas were unlike those generally eaten by other primates. However, at Lope chimpanzees and parrots also ate Duboscia when other fruits were scarce.

At Lope gorillas ate fibrous fruits in much smaller quantities when succulent fruits were abundant, as the latter were more nutritious, and fibre has a depleting effect on protein digestion in non-ruminants (see Milton 1979). However, Duboscia and Klainedoxa both fruited outside the forest community peaks, and individual trees were not synchronised, so these species may have helped to sustain some populations of frugivores during times of fruit scarcity.

7. Overall Strategy

The gorillas' feeding strategy was to select succulent fruits, which were complemented nutritionally by the inclusion of other food-types in the diet. When less fruit was available there was a tendency to decrease the diversity of fruits eaten, and to increase the consumption of stem-fibre, leaves and bark.

An inverse relationship between fruit and stem-fibre intake could be interpreted in

physiological terms: the nutrients obtained from fruit may have determined the fibre quotient; less stem-fibre may have been required to meet nutritional demands if the diet was of a better quality when more succulent fruit was consumed. Also, as the proportion of poor quality (fibrous) fruit in the diet increased, the amount of protein obtained from fruit declined. The gorillas may have compensated for this by eating more leaves, as suggested by the positive correlation between leaves and fibrous fruit in the diet, whilst a negative correlation exists between leaves and succulent fruit.

In addition, morphological factors such as gut capacity may have restricted Aframomum consumption when large volumes of fruit were swallowed. Whichever factors determined stem-fibre intake, it seemed that more Aframomum was eaten when fruit availability was low, and similar arguments applied to the consumption of leaves.

Both fruits and leaves are good sources of protein, but fruit protein is most digestible, while leaf protein is most concentrated (Hladik, 1977). Fruits and structural plant parts also provided different elements in the diet, which were not interchangable. Janzen (1978:79) suggested that fruits may be mixed with leaves to "keep the entire intestinal charge moving at a desirable rate", and the combination of foods in the gut is also important for obtaining complementary amounts of essential nutrients, referred to as 'mix and match' by Milton (1982).

Janzen (1978:82) remarked that "We may never be able to determine which secondary compounds are detrimental to orang-utans and gorillas, but...it would seem safe to assume that the same processes (identified in other primates) underly feeding patterns for these rarer primates". At Lope food selection was influenced by a combination of factors, which were difficult to evaluate, but the present study suggested that the availability of succulent fruits, and competition for those resources were among the variables relevant to gorillas.

F. GORILLAS AS MEMBERS OF A FOREST COMMUNITY

1. Dietary Overlap

In Gabon a large number of frugivores are sympatric: 44% of the 126 mammal

species, or 82% of all primary consumers at M'passa were frugivorous (Emmons et al, 1983). In general, West African monkeys are 1.7 times more frugivorous than their eastern counterparts (Gautier-Hion, 1983), and if gorillas mirrored this trend, lowland gorillas would be expected to eat more fruit than mountain gorillas.

During the present study opportunistic data were collected on the fruits eaten by other frugivores, such as elephants, 6 species of monkeys, and 14 species of frugivorous hornbills, touracos, parrots, and pigeons identified at Lope (C.J. Henty, unpub.). No data were collected for some other terrestrial mammals, such as duikers and bush-pigs. Scrutiny of the inventory of fruits eaten by gorillas revealed a high degree of overlap with chimpanzees (80.8%, N = 63 species), and elephants (47.4%, N = 37). Fewer species were confirmed for monkeys (35.9%, N = 28), and birds 9.0% (N = 7). Only 11.5% of fruits (N = 9) were not known to be eaten by other frugivores, however these species were rare in the habitat, and it was unlikely that they were foods unique to gorillas. Of the 69 'shared' fruit species, at least 3 of the 5 classes of frugivores (gorillas, chimpanzees, monkeys, elephants, and birds) ate 47%, 4 or more shared 30%, and the remainder were shared by all groups. The high degree of dietary overlap between fruit-eaters indicated the potential for competition within the community at Lope.

Gorillas at Lope ate 87.5% of the fruit species eaten by 3 classes of frugivorous mammals at M'passa, including fruits from both broad groups identified by Gautier-Hion et al (1985b): the brightly coloured succulent 'bird-monkey' fruits, and the large, dull, fibrous 'ruminant-rodent-elephant' fruits. Having classified these syndromes, Gautier-Hion and colleagues acceded that there was little specificity between plant species and consumers, and no specialist frugivores. Primates in Borneo were also generalists, although some niche separation was achieved by feeding specialisations: squirrels, parrots and pigeons were seed predators, hornbills and barbets preferred lipid-rich fruits, while bearded pigs ate mainly large fruits (Leighton & Leighton, 1983).

Dietary overlap between some Cercopithecus monkeys is so extensive that differences between males and females may be greater than those found between species; variance was greatest when fruit availability was low, and alternatives to preferred fruits were sought (Gautier-Hion, 1980). All monkeys supplemented their diets with

stems, leaves, bark, or insects. The importance of each fruit species in the consumers' diets was not considered in this evaluation, although several 'major' gorilla fruits were also preferred foods of moustached monkeys (Sourd & Gautier-Hion, 1986).

2. Competition

In all tropical forest communities studied so far the total amount of potential food produced per unit area per annum is small (Bourliere, 1979), and frugivore biomasses are determined by the minimum level of fruit production (Hladik & Chivers, 1978). Crop failures have occurred at Lope, and at others sites (e.g. Hladik, 1978; Gautier-Hion, 1980), and in Gabon the critical period was the major dry season, from April to August (Gautier-Hion et al, 1985a). Interannual variation in tropical forests is marked (e.g. Foster, 1982a; Gautier-Hion et al, 1985a; Rijksen,1978) and unpredictable fruit shortages have resulted in famines (Foster, 1982b). Tree species which fruit at irregular intervals throughout the year, and are not synchronised in their production, help to maintain frugivore populations, as has been shown in the tropical forests of Borneo (Leighton & Leighton, 1983).

Competition may be alleviated by changes in the diet or changes in food searching strategies; frugivores may use different parts of their range, or move further between sources each day. In Borneo hornbills emigrated (Leighton & Leighton, 1983), and male orang-utans moved out of their core-areas (Galdikas, 1979), while in Cameroon an influx of crowned guenons was noted when fruit was abundant (Gartlan & Strusaker, 1972). Diet could be modified by reducing selectivity, or by increasing the proportion of non-fruit foods consumed. When primates adjust their choice of foods, dietary overlap is usually reduced. In north-east Gabon chimpanzees increased their consumption of leaves and stems from 15% to 40% (Hladik (1973), and leaf intake by 6 species of monkeys almost doubled during the main dry season, even though new-leaf production was low (Gautier-Hion, 1983). Mandrills in Cameroon ate more leaves when less fruit was available (Hoshino, 1985), while orang-utans consumed more bark (MacKinnon, 1974; Galdikas, 1979), foliage (Rijksen, 1978), or both (Rodman, 1977).

At Lope elephants and large groups of chimpanzees were seen more often in the

study-area when fruit was abundant. Competition between the closely related chimpanzees and gorillas is of particular interest. Jones and Sabater Pi (1971) claimed that gorillas and chimpanzees depended on different food-types, and that vertical stratification of mitigated their feeding competition. However no such separation occurred at Lope: gorillas and chimpanzees fed in the same fruit trees within 24 hours of each other on several occasions, and a study in north-east Gabon demonstrated a 60% overlap in the fruit species eaten by both species of apes (Tutin & Fernandez, 1985). The main difference between the apes' diets was that the lipid-rich fruits mentioned above were of greater significance to chimpanzees, whereas fibrous fruits and large fruits, such as Pentadesma butyracea, were more important to gorillas.

Besides chimpanzees, the gorillas' most important competitors at Lope were elephants and mandrills. Monkeys, including mandrills, fed in trees where gorillas had been feeding earlier the same day, so direct competition for fruit sources probably occurred.

The food-species of mandrills in Gabon listed by Lahm (1986) suggest a fruit-diet overlap of at least 41% with gorillas, and in Cameroon fruit composed 84% dry weight of mandrills' faeces (Hoshino, 1985). Calvert (1985) noted that all of the gorillas' major foods were also eaten by other primates or elephants.

Whilst the above assessment was concerned with fruit, many forest species also fed on herbaceous plants: some monkeys (e.g. moustached monkeys, Sourd & Gautier-Hion, 1986; mandrills, Lahm, 1986), and large terrestrial mammals at Lope ate Marantaceae and Aframomum. Marantochloa was also eaten by elephants, buffalo, and probably chevrotains and sitatungas. Unlike fruit sources, competition for herbaceous foods was likely to be minimal, as they were plentiful and available all year round.

3. Competitive Abilities

Subtle differences in diet are important for allowing the coexistence of several primate species in the same area of forest. Differential exploitation of fruit sources by sympatric primates is related to differences in their morphology and physiology. The Cercopithicines have a physiological advantage over the apes, as they developed a

capacity to tolerate secondary compounds during a folivorous phase in their evolution, which allows them to eat unripe fruits before they are edible to gorillas (Andrews & Aiello, 1984). Gorillas have an advantage in their strength, which allows them access to resources which are not generally available to other frugivores. For example, they can eat large or heavy fruits, such as Detarium macrocarpum and Pentadesma butyracea, which are not within the processing capabilities of monkeys. Also gorillas can break branches to bring seemingly inaccessible fruits within reach.

The ability to adapt as supplies of fruit diminish is essential, and it is during periods of stress that competition between frugivores becomes acute. "If competition is important...body size should be considered as a possible mechanism by which niche separation in herbivorous communities is achieved" as the ratio between metabolic rate and gut capacity decreases with size (Demment, 1983:231), and the large body size of gorillas may result in a greater resistance to short-term food shortages, by permitting a dietary switch to low quality foods (cf. Wheatley, 1987).

In conclusion, gorillas at Lope seemed to be competing with a number of sympatric frugivores over sources of succulent fruit. Gorillas and chimpanzees were able to coexist even though their diets were very similar. It was only during periods of stress, when fruit was less abundant, that the apes' feeding strategies diverged to any large degree; competition was probably ameliorated by the gorillas' tendency to eat more stems, leaves, and fibrous fruits during periods of fruit scarcity.

G. COMPARATIVE STUDIES

1. Gorillas

Table 4.6 summarises information from all major field studies of gorillas. There are sharp contrasts between eastern gorillas and the western gorillas of the present study with respect to fruit. The number of fruit species recorded ranged from 1 for mountain gorillas, through 52 for western gorillas in Equatorial Guinea, to 78 at Lope. Fruit represented 1.4% of the gorillas' diet at Karisoke, about 40% of food-items in Equatorial Guinea, and 56% of foods items at Lope, where fruit remains were found in 98% faecal

Table 4.6 Feeding Data from All Major Field Studies of Gorillas

	NO.FOOD SPECIES	NO.FOOD ITEMS	NO.FRUIT SPECIES	FRUIT PORTION OF DIET
Mountain Gorillas				
Schaller, 1963	29	-	3	6.1% items
Schaller, 1963	27	-	3	10.0% items
Fossey & Harcourt, 1977	42	-	?	1.7% records
Vedder, 1984 (one group)	21	30	1	3.3% items 0.4% time
Watts, 1984 (one group)	38	75	3	4.0% items 0.3% time
Eastern Lowland Gorillas				
Schaller, 1963	12	-	0	0%
Casimir, 1975 (one group)	57 *	70	2	3.0% items
Goodall, 1977 (one group)	78	160	3	2.0% items
Western Lowland Gorillas				
Sabater Pi, 1977 (Equatorial Guinea)	92	128	52	56.5% species 40.6% items
Calvert, 1985 (Cameroon)	51	79	21	41.2% species 26.6% items
Tutin & Fernandez, 1985 (Gabon)	86	104	72	83.7% species 69.2% items
present study (Gabon)	103	139	78	75.7% species 56.1% items

* 56 food-species from Casimir's lists, plus Myrianthus from text

samples. The studies by Sabater Pi (1977) and Calvert (1985), in predominantly secondary areas of forest with little fruit, yielded intermediate values. Sabater Pi (1977) omitted 4 important food-species in Table 1 from Figure 8. These species were taken into account in the present evaluation. Unidentified foods from all studies were excluded].

Even with an emphasis on 'secondary' foods and on the gorillas' "inability" to climb, Sabater Pi (1977) concluded that lowland gorillas were more frugivorous than mountain gorillas. In Equatorial Guinea Uapaca guineensis fruit composed 10% of one gorilla's stomach contents (Sabater Pi, 1960, cited in Schaller, 1963:152), and when fruit was abundant fruits formed more than 50% of the diet (Sabater Pi, 1966b). The present study has demonstrated that gorillas living in mature forest depended primarily on fruits, although the precise proportions remain to be determined.

Mountain gorillas were both highly specialised and highly selective (Watts, 1984). The relatively rich montane habitat imposed few limitations on food availability, and competition was virtually negligible, therefore mountain gorillas did not need to seek alternative food sources. As well as being richer in nutrients, montane foliage was more digestible than that of tropical forests, containing less fibre and fewer secondary compounds (Waterman et al, 1983).

At Kahuzi-Biega and at Karisoke at least 80% of the gorillas' diet consisted of the leaves and stems of only 4 plant species: Galium simense (vines), Peucedanum linderi (celery) Carduus afromontanus (thistles), and Laportea alatipes (Goodall, 1974:135; Watts, 1984), whereas the gorillas at Lope ate a wide range of foods, including many succulent fruits. Thus there was little parity between the diets of the eastern and western subspecies of gorillas.

2. Other Frugivorous Apes

Frugivory is a basic dietary pattern among the primates (Wrangham, 1979; Andrews & Aiello, 1984). "The term frugivore signifies an animal that eats a high percentage of fruit" (Kay, 1984:25), but the division between frugivores and folivores is an oversimplification of a wide range of feeding strategies exibited by primates, which "inadequately characterizes dietary shifts" (Kay, 1981:143). However as chimpanzees

and orang-utans are generally described as frugivores (e.g. Galdikas, 1979; Ghilieri, 1987; Wrangham, 1986), the following discussion attempts to place the lowland gorilla within these arbitrary boundaries.

The proportions of fruit eaten by some populations of chimpanzees and orang-utans are given in Table 4.7. The variation in fruit intake was large, for example, fruit formed less than 50% of the orang-utans' diet for as much as half of the year (Rodman, 1977), and fruit in the diet of chimpanzees ranged from 55-80% (Hladik, 1973). Although fruit-eating by gorillas at Lope could not be quantified in relation to other food-types, some of the parameters used to describe the diets of other apes provide 'yard sticks' for comparison (Table 4.8). Differences between the apes' habitats were not taken into account, however, the gorillas were equivalent to their counterparts for these measures at least.

Table 4.9 presents Dietary Overlap Indices (DOIs), which were calculated using the procedure for SOIs (see Chapter 3). SOIs are also given, where available. DOIs were derived from data from areas that are floristically dissimilar to Lope, but they showed virtually no overlap with eastern gorillas, intermediate overlap with data from Sabater Pi (1977) and Calvert (1985); most similarities were found with chimpanzees. The lowland gorillas' dietary overlap with Pan paniscus is greater than with Pan troglodytes. The bonobos use of stems and shoots, particularly of Marantaceae, resembles their use by gorillas at Lope (e.g. Badrian & Malenky, 1984; Kano & Mulavwa, 1984). Wrangham (1986:377) even suggested that bonobos have taken advantage of the vacant gorilla niche south of the Zaire river.

The species-use and preferred food-types of lowland gorillas at Lope suggest that the lowland gorillas' general foraging strategy closely resembles that of the other frugivorous apes. Thus they differ greatly from the eastern subspecies of gorilla, which are so well known, and from whom many generalisations have been made. Ghiglieri (1987) stated that the proportional representation of food-types is similar for bonobos, chimpanzees and orang-utans, and I suggest that the same is true of lowland gorillas living in mature forest.

Table 4.7 Fruit Proportion of the Diet of Some Chimpanzee and Orang-Utan Populations

STUDY	FRUIT IN DIET	RANGE
Orang-utans		
Rodman, 1977	54% feeding time	13-89%
Rijksen, 1978	58% " "	
Galdikas, 1981	61% " "	
Chimpanzees		
Hladik, 1977	68% dry weight	55-80% *
Ghiglieri, 1984a	78% feeding time	

* chimpanzees' diet supplemented with bananas

Table 4.8 Some Measures of Frugivory

	Chimpanzees (Wrangham, 1977)	Lope Gorillas
Number of fruit species eaten:	68	78
Fruit proportion of food-items:	49%	56%
	Orang-Utans (Galdikas, 1982)	**Lope Gorillas**
Number of fruit seeds per faecal sample:	111	57 *
Number of fruit species per faecal sample:	2.5	3.0
Proportion of faecal samples containing fruit:	94%	98%
	(Rijksen, 1978)	
Proportion of fruit-species produced by trees	53%	57% (73% fruits)

* excludes 1000s of seeds < 1mm, e.g. Ficus, Nauclea

Table 4.9 Dietary Overlap Indices

SPECIES	NO.OF PLANT SPECIES	D.O.I. *	S.O.I. *
Mountain Gorilla			
Schaller, 1963 (Kabara)	29	0%	
Schaller, 1963 (Kayonza)	27	5.6%	
Vedder, 1984	21	0%	
Watts, 1984	38	0%	
Eastern Lowland Gorilla			
Schaller, 1963	12	8.3%	
Casimir, 1975	57	1.8%	4.3%
Goodall, 1974 (one group)	78	1.4%	
Western Lowland Gorilla			
Sabater Pi, 1977	92	21.0%	38.2%
Calvert, 1985	51	20.6%	23.1%
Tutin & Fernandez, 1985	86	33.3%	39.8%
Chimpanzees			
Ghiglieri, 1984	20	12.5%	
Reynolds & Reynolds, 1965	35	13.8%	15.7%
Sugiyama & Koman, 1987	156	14.4%	
Nishida & Uehara, 1983	198	7.3%	
Wrangham, 1975	149	5.9%	6.7%
Bonobos			
Badrian & Malenky, 1984 (Lomako)	76	23.7%	29.2%
Kano, 1983 (Yalosidi)	35	21.4%	
Kano & Mulavwa, 1984 (Wamba)	100	19.5%	35.4%

* see text and Table 3.5 for explanation

H. DISCUSSION & CONCLUSIONS

The gorillas' diet has been described as "the poorest known" for primates in nutritional terms (Gaulin, 1979). This is not true for the western lowland subspecies: during the present study the gorillas ate 139 plant foods of 103 species, including 78 fruits. Earth and invertebrates were consumed, of which weaver ants were the most important. Vegetative parts of Aframomum and Marantaceae formed staple foods, as they were abundant, accessible, and available year-round. Gorillas selected particular food-types and plant species, but they were generalists with respect to succulent fruit, which formed 91% of the fruit diet. From the volumes of fruits consumed it was estimated that 72% were gathered in trees. The fruit diet was diverse as a product of the heterogeneous nature of the habitat. Significant variation was measured in all parameters of the diet, reflecting seasonal rhythms in primary production. The availability of preferred fruits strongly influenced the composition of the diet, and flexible foraging strategies enabled the gorillas to cope with fruit scarcity, particularly during the major dry season.

The gorillas body size is also important in determining its foraging strategy, as body size determines nutritional requirements. Large mammals are physiologically better equipped to withstand food shortages as a result of their relatively low metabolic rates (e.g. Gaulin, 1979). If food availability fell below a critical level, a poorer quality diet would have been tenable for gorillas as a result of their large body size. The poorer quality fibrous foods, including fibrous fruits, could have provided an adequate buffer when fruit was scarce at Lope. Thus the gorillas' capacity to switch to a poorer quality diet may have been permitted by their large body size, and related allometric scaling of metabolic requirements (e.g. Gaulin, 1979; Wheatley, 1987), which will be further discussed in Chapter 8.

Heterogeneous tropical habitats provide quite different conditions to those experienced by mountain gorillas. At Karisoke many food-species occurred at high density, and there was a low variability in food-patch size (Watts, 1984). In forests most species occur at low densities, and this has direct consequences for food selection. Foraging theories predict that when food density is low the diet will be more diverse (e.g. Gaulin, 1979). Another characteristic of the mountain gorillas' food supply is the near

absence of significant temporal variation in availability and abundance (Watts, 1983:418). Seasonal production and the emphemeral quality of many foods have profound effects on feeding strategies. Eastern lowland gorillas were selective towards fruits, as Myrianthus and Pygium fruits were eaten in large quantities when available, but fruits were rare in the montane habitat (Goodall, 1977). Goodall (1977) found that the minor differences in seasonality between Kahuzi-Biega and Karisoke resulted in the gorillas eating a more diverse diet at the former site. Thus the conditions presented by lowland tropical forests contrasted those of the mountain gorillas' Virunga Volcanoes habitat (Chapter 3), and food selection by gorillas at Lope differed accordingly. Diverse forest habitats are unpredictable, and some of the problems of food location will be discussed in Chapters 6 and 8.

The genus Gorilla has long been misrepresented as a folivore. This study redresses the balance somewhat by giving new data on a primarily frugivorous lowland gorilla population in a tropical forest habitat.

CHAPTER 5: NESTS AND NESTING

A. INTRODUCTION

Nest-building was mentioned in the earliest published reports of gorillas (e.g. Battell, 1613, cited in Yerkes & Yerkes, 1929; Savage & Wyman, 1847). Although reports by travellers contained many misconceptions, Du Chaillu described the basic method of nest-building correctly in 1861, as did Donisthorpe (1958) and Bolwig (1959) in subsequent studies. More recently Schaller (1963) and Goodall (1974) have investigated nest-building by eastern gorillas in detail, but there has been little systematic study of western gorillas' nests, with the exception of Jones and Sabater Pi (1971).

All weaned gorillas make a nest each night, which is usually a cushion of vegetation. Juveniles sleep with their mothers until they are 2.5 to 3 years old. Infants have been seen to manipulate vegetation at 8 months of age, and to build clumsy nests by 18 months, although these nests were not slept in (Fossey, 1979). A gorilla's nest serves the functions of a bed, and thus differs from nests built by other mammals whose nests form a "home" or "fix-point" (Hediger, 1977), and are important for rearing young. Prosimians build nests, but great apes are the only simians to do so.

Gorillas build a new nest every evening and rarely re-use the same nest, as noted by many writers (e.g. Anon, 1934; Bolwig, 1959; Donisthorpe, 1958; March; 1957; Maxwell, 1928), and confirmed by recent studies (e.g. Goodall, 1974:141; Jones & Sabater Pi, 1971; Schaller, 1963:171). Dyce Sharpe's (1927) description of a group confined to an island for a week illustrates this nicely: the gorillas constructed fresh nests each night, within a few metres of nests from previous nights, some within the same tree. Only 2 "possible" incidences of nest re-use have been reported (Sabater Pi, 1960; Goodall, 1974:141).

Nests provide valuable clues to group size and composition, habitat use and range size, and are a source of dung: half the quantity of faeces produced daily may be associated with nests (Schaller, 1963:201). A distinction is generally made between night-nests and day-nests. The latter, first described by Bingham (1932), are built as resting places between bouts of feeding, and most are made during the mid- to late-morning rest period. In this chapter the basic features of nests and nest-sites are

described and compared with data from other populations.

B. NEST-SITES

A nest-site is an area of the habitat encompassed by a collection of nests, usually in close proximity, which were built on the same night by a single group of gorillas.

1. Number of Nests

The number of nests which made up 113 sites ranged from 1 to 19. These were built by at least 9 groups; 13 sites had been occupied by solitary males. Sometimes a partially or completely constructed nest was abandoned and another produced. Such nests were identifiable because the nest material had not been crushed. Of 991 nests only 16 had not been slept in (1.6%). These were not included in nest counts. Unused nests were rare at Kabara (1.6%, N = 3052, Schaller, 1963:182), and at Kahuzi-Biega (0.1%, N = 1116, Goodall, 1974:141).

2. Dimensions of Nest-Sites

The shape of nest-sites was influenced by the terrain, vegetation, and the position of peripheral animals (cf. Goodall, 1974:138). Some were roughly circular or rectangular, many were irregularly shaped. Groups nesting on steep slopes used supports, such as tree trunks or logs, to avoid sliding downhill. At one site, 5 out of the 7 nests were lined up against the same log.

Casimir (1979) described a tendency for nest-site areas to increase with the number of ground-nests, and Elliot (1976) recorded a reduction in site diameter when group size fell from 4 to 3 individuals (although no expansion occurred with a subsequent increase in group size). Groves and Sabater Pi (1985) dismissed this relationship between the number of gorillas and area of the nest-site, argueing that Casimir's correlation was caused by peripheral males forming temporary associations with groups. However, in the present study a similar correlation was found between the number of nests and nest-site areas. The area of an elipse was calculated (cf. Casimir, 1979) using the formula:

site-length x site-width x 3.142 x 0.25

where:

SITE-WIDTH = the largest distance between 2 nests on a line perpendicular to the site-length;

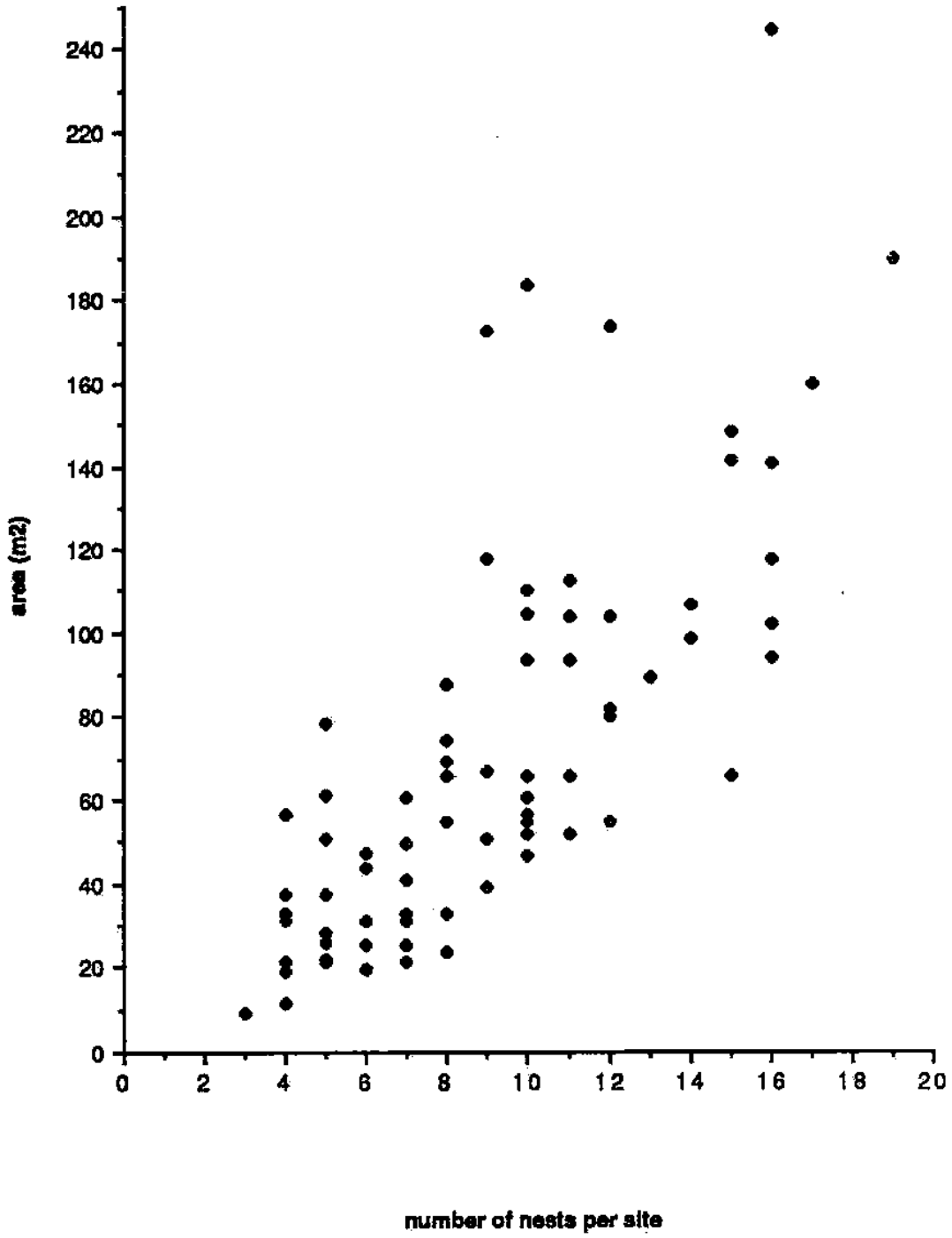
SITE-LENGTH = the largest distance between any 2 nests in the group.

The significant correlation between site-area and group size ($R(77)=.756$, $p<.001$) was independent of any single outlying nest, implying that the area required to nest increased with the number of animals in a group. This trend is illustrated in Figure 5.1, which shows the distribution of all nest-site areas in relation to the number of nests per site. The mean area of 77 nest-sites was 75.3 m^2 (sd = 49.3), mean site-length was 12.8 m (sd = 4.4), and mean site-width was 7.0 m (sd = 2.7). Apart from Casimir's systematic analysis of nest-site areas, only qualitative estimates have been published. These include 150-700 m^2 (Jones& Sabater Pi, 1971) and 160-170 m^2 (Groves& Sabater Pi, 1985) for the same data set. Judging from Figure 6 in Casimir's paper, the areas of nest-sites at Mt. Kahuzi were considerably larger than those found at Lope. The largest estimate from Zaire was about 540 m^2, almost twice that from Lope: 245 m^2. Casimir's median value for sites with 10 nests was about 100 m^2, compared to 60 m^2 at Lope. These differences were probably related to the physiognomy of the vegetation; at Lope gorillas may have nested closer together to avoid separation by the high density of trees in the forest (Chapter 3).

3. Spatial Arrangement

At Lope the position of all nests at each site was mapped, but their arrangements have not been analysed, as only one nest per group could be reliably identified: careful searching of the nest material usually revealed a few long, grey-banded hairs in beds which had been occupied by adult males. The silverbacks did not seem to have favoured locations, and their nests were found at various positions relative to the other group members. The early literature contains many claims about nest formations and, in particular, the position of the silverback. It has been stated that the leading male choses a position of strategic defense, often nesting at the base of a tree in which the females and young sleep together (e.g. Allen, 1931; Aschemeier, 1922; Derochette, 1941; Valker, 1931).

Figure 5.1 Areas of Nest-Sites at Lope (N = 77)



Schaller (1963:181) and Goodall (1974:138) found no consistent patterns at eastern gorillas' nest-sites. Both found that an individual's position within the group was variable, and that sub-groups existed at some sites. Fossey (1983:176) and Schaller (1963:184) noted that independent juveniles tended to sleep next to their mothers, or near to silverbacks, whilst blackbacks nested peripherally. Casimir's (1979) study of 63 sites built by one group led him to conclude that nest configuration was random and independent of an individual's age and sex. Pitman (1935) proposed that positions were selected for visual contact between group members, however Groves and Sabater Pi (1985) reported that "some" nests were hidden from the remainder of their social group, and at Lope nests were often visually isolated by thick vegetation. It is possible that gorillas prefer to nest near to particular individuals in a group, but it should be remembered that the silverback usually initiates nest-building and that other group members place themselves around him (Schaller, 1963:183).

C. INDIVIDUAL NESTS

The characteristics of 748 nests were recorded, but analyses were restricted to those nests which showed little sign of deterioration (N = 663).

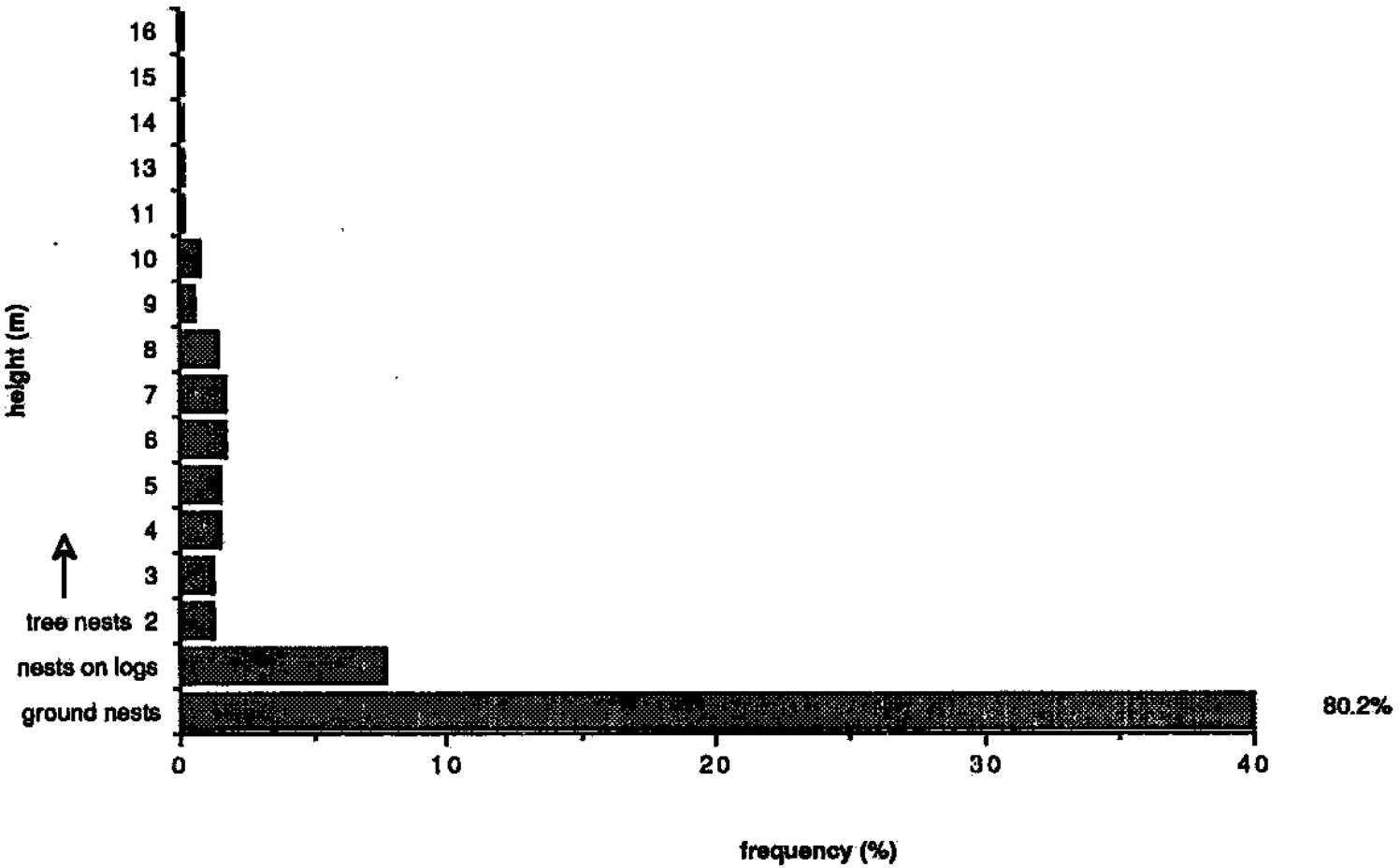
1. Nest Height

Nests were found at ground level and in the foliage of shrubs or trees. Nests in trees were differentiated from other nests located above ground, but on logs. Figure 5.2 shows the height distribution of all nests.

a) Ground-Nests.

Ground-nests formed 80.2% of the sample (N = 532). Some were positioned against the trunks of saplings or trees (1.9%, N = 10) or logs (0.6%, N = 3). In other studies silverbacks "frequently" used trees (Donisthorpe, 1958; Bolwig, 1959) or buttress roots (Ischac, 1938; Blancou, 1955) as backrests. Casimir (1979) found that 27.0% of silverbacks' nests were located at bases of large trees, but no such tendency was seen at Lope.

Figure 5.2 Heights of gorillas' nests at Lope (N = 663)



b) Nests Above Ground.

Nests built off the ground, but not in trees, formed 7.7% of all nests, or 38.9% of nests above ground (N = 51). Most were found on trunks of fallen trees, with 2 exceptions which were built on mounds of earth. Mountain gorillas often build nests on logs, on buttresses of Hagenia trees, in the low crotches of large trees and in bamboo (Goodall, 1974:139; Kawai & Misuhara, 1959; Schaller, 1963:188). Bingham (1932) noted that cavities in large trunks were favoured sleeping sites, and Fossey (1983:47) found that gorillas tended to use such hollows during the rainy season. Other studies of western gorillas recorded similar proportions of nests built on logs (8% Tutin & Fernandez, 1983b; 11% Groves & Sabater Pi, 1985), but no unusual locations have been reported for this subspecies.

c) Tree-Nests.

Tree-nests formed 11.8% of all nests (N = 78). Usually only one nest was built in any single tree; only 11 pairs and 2 triplets of nests were found within the same tree.

i) Frequency of Tree-Nests. The reported occurrence of tree-nests ranges from Merfield (1954) who never saw a tree-nest, to Pitman (1935) who described ground-nests as exceptions to the rule. At Lope the ratio of tree-nests to ground-nests varied between seasons: tree-nests were significantly more common during the wet season (dry: 5.2%, wet: 13.8%; F= 8.63, p=.003). This trend may have resulted from the gorillas' avoidance of damp ground, which may also have accounted for the higher proportion of tree-nests found in seasonally inundated forest compared to other habitat types in Gabon (Tutin & Fernandez, 1981).

Only 11 tree-nests could be assigned to age-sex classes (8 juvenile; 2 adult; 1 female with infant) as classifications were made from the diameter of dung. But the dung associated with tree-nests was generally inaccessible, or had been splattered by the fall to the ground. The small sample suggested that most tree-nests were constructed by juveniles. This was also indicated by a comparison of the dimensions of all tree-nests with ground-nests: the former were significantly smaller (F= 7.124, p=.008). Bingham (1932) attributed most tree-nests to juveniles and subadults, Schaller (1963:181) found that juveniles built twice as many tree-nests as females or blackbacks. Goodall (1974:160)

identified tree-nests which had been built by females with infants, but none by silverbacks, although silverbacks' nests have been found above ground by Bolwig (1959) and Schaller (1963:181). Most authors explained this age-class stratification in terms of body-weight and the availability of sturdy trees (e.g. Donisthorpe, 1958; Kawai & Misuhara, 1959).

ii) Height of Tree-Nests. The mean height tree-nests was 6.3m (N = 77, sd = 2.8, range = 2-16m). Most were built between 3 m and 8 m above ground (see Figure 5.2).

A significant correlation between the heights of nests and of trees was predictable, given that the size of a tree was a limiting factor ($r(82)=.82$, $p<.001$). Nest-height would have been influenced by the height, branch arrangement, and foliage of trees. Chimpanzees in Senegal built nests at around 80% of the trees' height (Baldwin, 1979:140). The Lope data yielded a similar value (median = 82%), but the range was large (25-100%). Nests in larger trees were usually positioned on side branches, and rarely seen in forks, as has been reported from Nigeria (Anon, 1934) and Equatorial Guinea (Jones & Sabater Pi, 1971). Many nests were built at the tops of small trees, incorporating the entire canopy.

There seems to be considerable local variation in the vertical distribution of nests across all populations of gorillas studied (Table 5.1). Reichenow (1920, cited in Yerkes & Yerkes, 1929) proposed that racial differences could be found with regard to nesting in trees: based on his own observations in Cameroon and those of von Koppenfels in Gabon, he claimed that in Gabon many nests were built in trees, but that in Cameroon most nests were found on the ground or in low bushes. Data from the present study do not agree with this statement, as tree-nests at Lope were rare compared with other regions, and in Cameroon gorillas' nested as high as 12 m in trees (Critchley, 1968).

The maximum heights reported rarely exceeded 16 m, except in the Tshibinda region of Zaire, where about 2.6% of nests were found between 17 m and 30 m (Goodall, 1974:291). In all areas gorillas nested at low levels relative to chimpanzees (Schaller, 1963:374; Tutin & Fernandez, 1983a). Comparative data for chimpanzees are available from Equatorial Guinea (Jones & Sabater Pi, 1971), Senegal (Baldwin, 1979), Liberia (Anderson et al, 1983), Gabon (Tutin & Fernandez, 1983a), and Zaire (Kano, 1983).

Table 5.1 Height in Metres of Gorillas' Nests

SITE		N	0 m	1 m	2-10	>10	maximum
Eastern Populations							
Kabara	(Schaller, 1963)	2488	97.1%	0.2%	2.7%	0%	9 m
Utu	(Schaller, 1963)	110	21.8%	1.8%	55.5%	20.9%	16 m
Tshibinda	(Goodall, 1974)	915	46.8%	10.9%	28.1%	14.0%	18 m
Nyakalonge	(Goodall, 1974)	202	76.6%	7.9%	12.1%	2.8%	30 m
Mt. Kahuzi	(Casimir, 1979)	724	68.8%	4.5%	23.5%	3.3%	15 m
Western Populations							
Eq. Guinea	(Groves & Sabater Pi, 1985)	448	77.9%	11.2%	10.5%	0.5%	15 m
Gabon	(Tutin & Fernandez, 1983)	1022	71.6%	7.9%	18.5%	2.0%	16 m
Lope	(present study)	663	80.2%	7.7%	11.6%	0.8%	16 m

2. Nest Size

Nests were usually round or oval-shaped in outline, as described by Schaller (1963:182) and Groves & Sabater Pi (1985). Data on nest diameters for 3 age-sex classes are presented in Table 5.2, with comparative data, which were found to be very similar. In the present study 3 dimensions of nests were measured (i.e. length, width, depth), and areas calculated for (i) all ground-nests, (ii) all tree-nests, and (iii) ground-nests which had been assigned to age-sex classes (Figure 5.3).

Nest size tends to be related to body size of the builder and their arm's reach, as apes form nests around their bodies (see below). Bingham (1932) used nest size to differentiate age-sex classes, and Schaller (1963:182) agreed that certain classes could be identified if corroborated by dung. In the present study the areas of nests built by each age-sex class were distinct ($F= 19.488$, $p<.001$), but there was much overlap between them, so nest size alone was not a reliable criterion by which to categorize nest-builders.

A seasonal trend in the depth of nests was reported from Equatorial Guinea: during the wet season gorillas incorporated more leaves into their nests, suggesting that thicker nests were built to prevent body contact with wet ground (Groves & Sabater Pi, 1985). At Lope the depth of nests did not differ between seasons ($F=.014$, $p=.906$).

3. Nest Construction

The basic types of nests were defined in Chapter 2, and the frequencies of each type are given in Figure 5.4. Herbaceous and 'mixed' nests comprised 95.5% of all ground-nests. Only 1.9% of ground-nests were minimally constructed. Nests built on logs were predominantly herbaceous or 'mixed'. 'Cave' and 'attached woody' were rare (< 1% entire sample) and they seemed to be anomalies. Most authors merely distinguished between ground- and tree-nests, although Groves and Sabater Pi (1985) defined 3 categories of ground-nest according to the substrate (i.e. flat ground, slope, bush, or tree).

Nests have been described as cup-shaped, with an emphasis on construction of the rim (Schaller, 1963:188; Fossey, 1983:47; Groves & Sabater Pi, 1985). At Lope nests were classified according to their components, rather than the resulting shape or form,

Table 5.2 Diameter (cm) of Gorillas' Nests in Relation to Age-Sex Class at Various Study-Sites (mean and standard deviation)

AGE-CLASS	present study (N = 211)	Casimir (1979) (N = 643)	Schaller (1963) (N = 76)	Groves & Sabater Pi (1985) (N = ?)
silverback	105 ± 14	127 ± 15	150	132
female + infant	102 ± 16	110 ± 13		
adult	93 ± 18	105 ± 12		115
juvenile	79 ± 20	79 ± 18	60	75

Table 5.3 Proportion of Nests With No Overhead Cover at Various Sites

SITE AND STUDY		N	%
Kabara, Zaire	(Schaller, 1963)	1837	92.6
Nyakalonge, Zaire	(Goodall, 1974)	202	72.5
Tshibinda, Zaire	(Goodall, 1974)	915	84.1
Equatorial Guinea	(Jones & Sabater Pi, 1971)	448	74.8
Lope, Gabon	(present study)	663	62.7

Figure 5.3 Size of Gorillas' Nests at Lope (mean ∓ standard deviation)

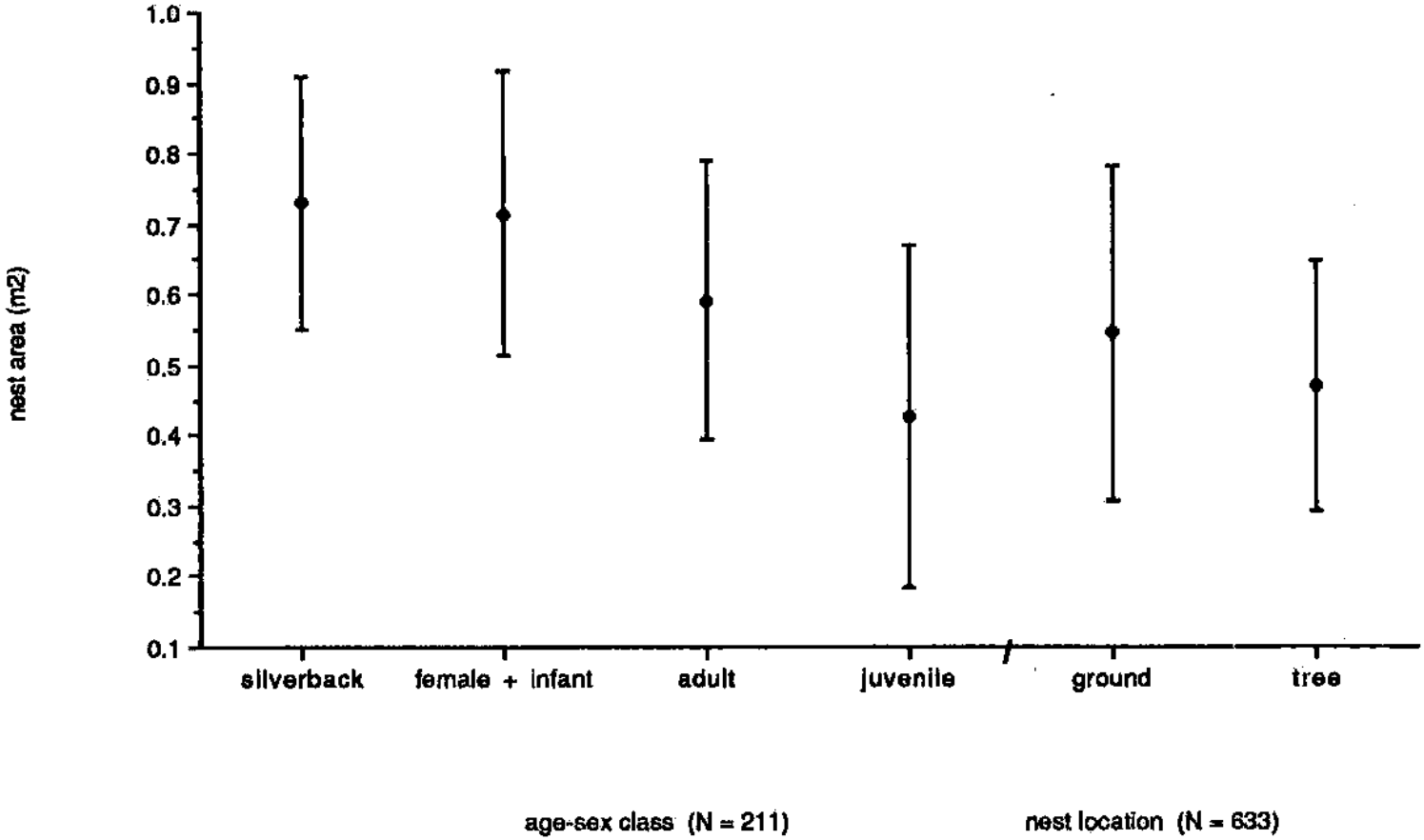
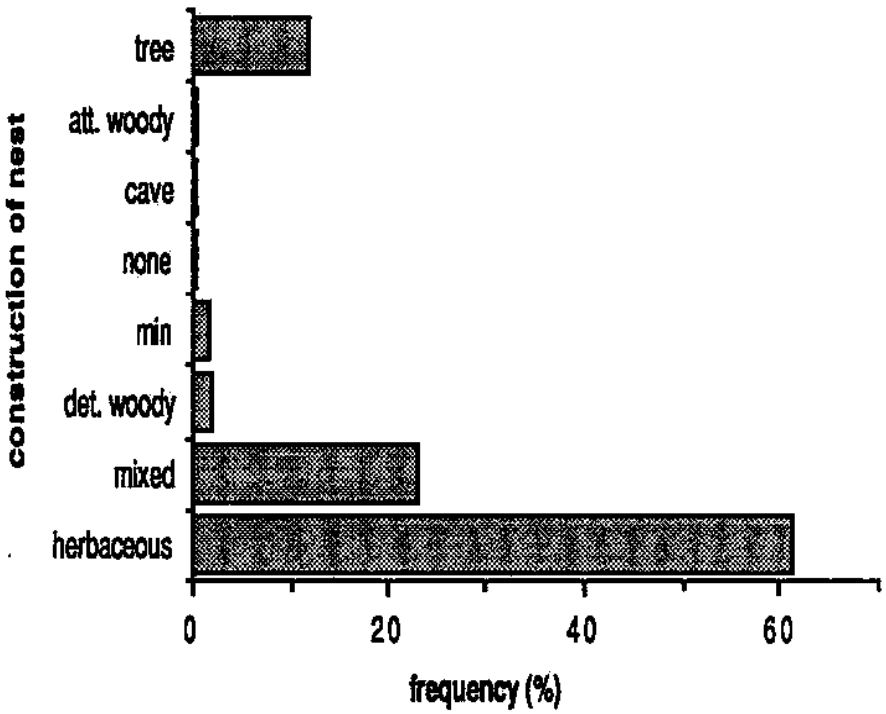


Figure 5.4 Types of gorillas' nests (N = 663)



Definitions of Nest Type

HERBACEOUS: many stems of herbaceous plants bent to form a platform with a roughly circular depression;
MIXED: mixed herbaceous and woody, similar to above, but with woody lianas, shrubs, or detached branches also incorporated into nest;
DET.WOODY (detached woody): nest constructed exclusively from woody branches broken from shrubs or trees;
MIN (minimal construction): few stems of herbaceous plants bent to form a rudimentary pad;
NONE (no construction): gorilla slept on bare ground;
CAVE: gorilla slept on bare earth, below a roof of vines;
ATT.WOODY (attached woody): formed from woody branches which were still attached to shrub or tree;
TREE: nest constructed above ground in a tree or shrub, formed by bending woody vegetation into a sleeping platform.

however, within this classification, 3 types of herbaceous nests were common:

(i) CUP AND RIM: cushions apparently shaped by the impression of the gorillas' weight, rather than by design;

(ii) MATTRESSES: piles of flattened vegetation of variable thickness (Figure 5.5);

(iii) VINE-TOWERS: bed formed by pulling down a wall of Marantaceae vines (Figure 5.6).

'Vine-tower' nests have not been described at other sites, although Schaller (1963:186) noted that masses of tangled vines were sometimes pulled together on the ground.

Bingham (1932) and Ischac (1938) published accurate descriptions of nest structure, and since then several lengthy accounts of nest-building techniques have appeared (e.g. Bolwig, 1959; Goodall, 1974; Schaller, 1963). Nest-building by wild gorillas was not observed during the present study, but the nests revealed that methods of construction resembled previous descriptions: typically an individual sits or stands on the spot and pulls vegetation towards itself. This is broken or bent around and under the body, and held in place by the gorilla's weight. The precise method used depends on the vegetation available and the nature of the substrate (Bolwig, 1959; Goodall, 1974; Schaller, 1963). Early reports also proposed that apes collected twigs or branches and carried them to the nest-site (e.g. Dyce Sharpe, 1927), and that nests were lined with leafy twigs and dead leaves (e.g. Osborn, 1963). Neither of these features were found during the present study and were rare at Kabara (Schaller, 1963:187). At Lope the nest vegetation almost always remained attached to the intact plant; the foliage of saplings used in 'mixed' nests was prevented from springing up again by snapping the trunks without detaching them. Many tree-nests were basin-shaped, although some were little more than dense tangles of small branches. Some descriptions have suggested that vegetation was woven together, but weaving not was seen at Lope, Kabara (Schaller, 1963:188), or Kahuzi-Biega (Goodall, 1974:160).

At Lope nests with minimal or no construction were rare (1.5% and 0.2%), while Schaller (1963:187) recorded 10% of nests without any definate structure. Goodall (1974:141) found that individual gorillas often slept without a nest, and that on 2

occasions an entire group did so. At Belinga, in north-east Gabon, 9.3% of nests were poorly constructed (Tutin & Fernandez, 1983a). The existence of such sleeping sites may only have been obvious from depressions in the soil and faeces nearby, thus they may not have been recognisable after about 4 days (Tutin & Fernandez, 1983a). If these 'nests' had been overlooked, the number of nests per site would have been underestimated, especially as well constructed nests remain visible for up to 6 months (mean duration = 54 days, Tutin & Fernandez, 1984). However, a comparison of the frequencies of each nest-type found at nest-sites of variable age revealed no significant differences ($F= 2.789$, $p=.095$).

Silverbacks and females with dependent offspring always made fairly elaborate nests, while juveniles built most of the minimal nests. These observations agree with Casimir (1979), who noted that females with infants rarely failed to build nests, and Schaller (1963:191) who stated that juveniles' nests were often crude. The majority of tree-nests were built by the smaller individuals, and not by silverbacks, as stated above.

One further note on nest construction relates to the slope of the ground at nest-sites: at some steep locations the gorillas constructed a barrier by anchoring and levelling off the vegetation, or propping the nest up against a tree trunk, to prevent themselves from sliding out of bed. Similar modifications were observed by Casimir (1979), and described in detail by Bolwig (1959).

4. Nest Materials

The plants identified in gorillas' nests belonged to at least 38 species, representing 22 families; 17.3% items were not identified. Marantaceae and Aframomum could not be identified to species level, and so were represented by 2 broad categories, thus 'items' shall be used in place of species from here on. All items were of 3 major types:

75% Marantaceae and Zingiberaceae

13% trees and saplings

12% other materials (shrubs, vines, grasses, dead wood)

The majority of ground-nests were constructed from 2 items, usually Aframomum and Marantaceae (52.3%); 95.4% contained less than 4, and the maximum

number recorded was 7. Tree-nests differed in that 88.5% were built from a single items, as few other materials were accessible from tree canopies. In total 8 nests (10.3%) were formed by pulling together 2 or 3 saplings. Only 1 tree-nest contained more than 3 items, which were foliage from 3 saplings, together with some vines. In Equatorial Guinea 68.1% of nests contained only 1 item, usually Aframomum, and only 3.7% included 5 or 6 items (Groves & Sabater Pi, 1985).

a) Ground-Nest Materials.

At Lope 25 species from 14 families were identified in ground-nests; 15.9% items were indeterminate; and 21 of all types were gorilla foods. The predominant items were Marantaceae and Aframomum, the gorillas' staple foods: 92.9% nests (N = 494) included Marantaceae, and 63.2% (N = 336) contained Aframomum. The high usage of these herbs was most likely due to their ubiquity, as they occurred at high densities throughout the study-area at Lope (Rogers & Williamson, 1987). Jones and Sabater Pi (1971) reported similar figures of 95.6% nests with Aframomum and 54.1% with Sarcophyrinium (Marantaceae), although Groves and Sabater Pi (1985) adjusted the same data to 81.7% Aframomum and 14.7% Sarcophyrinium. Tutin and Fernandez (1981) also reported that a high proportion of nests (98%) included Marantaceae and Zingiberaceae.

b) Tree-Nest Materials.

At Lope 13 of the species incorporated into tree-nests were identified, but 49.0% of trees and saplings were not. Besides foliage, only vines were included (N = 5).

The basic requirements for nest-trees are abundant soft foliage, preferably with small leaves, pliable branches, perhaps with fibres that snap and do not spring up again but that do not snap off completely, and a firm base, strong enough to resist collapse under the animals weight (Baldwin, 1979; Dixson, 1981; Schaller, 1963:180).

'Preferences' have been demonstrated in other studies by comparing species-use by apes with composition of the habitat (e.g. Anderson et al, 1983; Kano, 1983; Ghiglieri, 1984a). At Lope 39.7% of tree-nests were built in 4 species: Xylopia aethiopica, Xylopia sp., Diospyros dendo and Diospyros polystemon. These species were all abundant in the habitat, ranking in the 'top 10' species (see Chapter 3), but many other species were not suitable for nest-building. Aucoumea klaineana and Cola lizae, the top 2 ranking

species at Lope, were not selected. Aucoumea were large trees with thick trunks which made them difficult to climb; Cola had enormous leaves which were neither amenable to manipulation, nor comfortable. Cola saplings were only used in ground-nests.

Generally gorillas used any plant within arms reach as nest material. A lack of selectivity by gorillas has been the impression gained during previous studies (e.g. Casimir, 1979; Donisthorpe, 1958; Goodall, 1974:139; March, 1957). Thus species-use at different sites is not compared here, especially as Schaller (1963:186) emphasised that "an elaborate classification of nest material is of little value, for they vary from region to region and merely reflect the location".

5. Shelter

In this study a distinction was made between 'open' and 'closed' canopy overhead to indicate the degree of exposure to open sky or protection from rain. Jones and Sabater Pi (1971) and Goodall (1974:151) evaluated gorillas' nest-sites in relation to early morning sunshine. Any positive orientation towards the sun has been discounted by Goodall (1974:168) and Groves and Sabater Pi (1985). In tropical forest habitats, such as Lope, the ability of the sun to warm and dry sleeping individuals should not be overestimated: not only do gorillas become active soon after dawn (see Chapter 6), but sunlight is often blocked out by the canopy, or by heavy early morning mists. Sunlight could reach only those nests in fairly open areas, and rarely before mid-morning.

At Lope 62.7% of nests were 'open', but scores of 49.4% 'open' tree-nests and 69.6% 'open' ground-nests indicated that tree-nests were more sheltered ($F= 10.566$, $p<.001$), so tree-nests were excluded from further analyses. Comparative data are given in Table 5.3. The variation between sites is largely due to physiognomic differences in the vegetation; the mountain gorillas' habitat is more open than western gorillas' tropical forest (Goodall & Groves, 1977). The data from Equatorial Guinea were collected in predominantly secondary areas, where the canopy was probably low and uneven. It is interesting that Nyakalonge, in Zaire, has the most similar proportion of sheltered nests to the Lope; as an area of 'primary' montane forest it would also have the most similar physical structure. When evaluating the exposure of nest-sites, the conditions in forest

should be considered. The canopy may provide shelter from the full force of a storm, but after rainfall stops water continues to drip from leaves. Gorillas may therefore experience less discomfort if they nest in the open and rain ceases abruptly, than if they are subjected to water dripping from the vegetation for a prolonged period (cf. Baldwin et al. 1981). Goodall (1974:161) stated that gorillas disregarded shelter, as they generally nested in open areas, and the high proportion of 'open' nests found in all populations studied seems to support this view.

A comparison of scores from dry nights with nights when it was known to rain at Lope revealed no significant difference in shelter ($F=.506$, $p<.478$). However, a problem with these data was that the timing of rainfall was not known; if the gorillas had nested before rain started, it may not have influenced selection of the site. Schaller (1963:298) recorded rainfall between 16.30 hrs and 18.30 hrs, when mountain gorillas usually constructed their nests. He found that 4.7% were sheltered on dry nights, 18.5% when it rained, but that at least 80% of gorillas slept in exposed positions at all times. He concluded that the gorillas' responses to rain were inconsistent. Two other studies of eastern gorillas in open habitats found no seasonal differences in the degree of exposure (Casimir, 1979; Kawai & Misuhara, 1959). In Equatorial Guinea gorillas built more sheltered nests in the wet season, 32.6% compared to 20.1% in the dry season (Groves & Sabater Pi, 1985). Similar figures were obtained at Lope: 22.9% nests were 'closed' in the dry season, 35.7% in the wet season, however, the difference was not significant ($F=4.782$, $p=.029$).

The only record of gorillas sleeping under non-vegetative shelter came from a group of mountain gorillas which spent a night under a rocky ledge (Bingham, 1932). Overhead nest construction may be another form of shelter, though one rarely used at any site: at Lope only 2 "cave" nests were built, but these offered little protection. A similar structure was seen by Bingham (1932), and one further example was given by Groves and Sabater Pi (1985). The only African apes known to shelter by placing leafy branches across their bodies are bonobos (Kano, 1982).

Although the actual proportions of sheltered nests were variable, the same trend was found for all populations, even though it was not statistically significant at Lope: more

nests had overhead cover during the wet season. But the number of exposed nests was always high. Overall, shelter may be a secondary factor which should not be considered in isolation, as the the presence of suitable vegetation may be more important for the selection of nest-sites (see Goodall, 1974:161; Schaller, 1963:171).

6. Dung in Association With Nests

Several authors have commented on defaecation at nest-sites (e.g. Aschemeier, 1922; Bingham, 1932; Bolwig, 1959; Kawai & Misuhara, 1959), while recent studies have detailed the presence and position of faeces relative to the nest, and whether or not the dung had been lain on (Goodall, 1974:146; Schaller, 1963:196).

In the present study tree-nests were excluded from analyses as their interiors were inaccessible, although dung was found on the ground below 67.7% of fresh tree-nests. Of 517 ground-nests at Lope, 23.2% had faeces in the cup, 16.2% on the rim, 35.8% outside the nest, and no dung was found with 24.8%.

The reported frequency of soiled nests varies across populations, ranging from 18.0% at Mt. Kahuzi (Casimir, 1979) to 82.2% at Kisoro (Schaller, 1963:197), both in Zaire. In West Africa, Merfield (1954) claimed that in the dry season nests were always clean, but that they were frequently soiled on wet mornings when gorillas were loath to leave their nests. This tendancy was not confirmed by Groves and Sabater Pi (1985), although at Lope dung was absent from a greater proportion of nests in the dry season (17.8% wet season, 35.5% dry season; $F= 18.388$, $p<.001$).

At Lope dung was lain on in only 1.5% of nests, or 7.5% of nests with dung inside ($x = 9$). Schaller (1963:196) found that at Kabara all dung deposited inside nests had been flattened (73.1% of all nests); Goodall (1974:147) gave a figure of 14.2% for Tshibinda (I calculated 12.1% from his data), and Casimir (1979) found that in 8.7% nests dung had been lain on. The proportions of flattened dung were given as percentages of entire samples, but may be meaningful only as a proportion of nests which contained dung.

Goodall (1974:147) discovered regional trends in Zaire: at Tshibinda dung was flattened in 14.2% (54.0% nests with dung only); at Nyakalonge it was only 2.4% (33.0%). Attempts have been made to relate regional variations to altitude and

temperature, proposing that dung spread inside nests acted as an insulating layer when night temperatures fell below freezing (Goodall, 1974:148). However gorillas living at lower altitudes, where the cold was not so extreme, also lay on their dung (Schaller, 1963:197). As Groves and Sabater Pi (1985) rightly pointed out, there would be no thermal advantage if faeces were not eliminated until dawn, as seems to be the case.

An investigation of age-class differences revealed that deposition of dung outside the nest increased with age. I excluded nests with no dung, as determination of age-class required the examination of faeces. The variation was marked ($F= 12.102$, $p<.001$), with infants (57.8% nests soiled) and silverbacks (4.8%) forming the extremes. Similar trends were observed by Goodall (1974:147) and Casimir (1979). Goodall included all nests in analyses (1974:147) stating that juveniles flattened their dung least often, but this emphasis is lost if only nests with dung inside are considered. Goodall also noted that silverbacks at Mt. Kahuzi deliberately placed their rumps over the edge of the nest to defaecate.

The main difference between gorillas at Lope and elsewhere was that less dung was found in their nests. Western gorillas ate large quantities of fruit, and their dung was often soft, whilst that of eastern gorillas was firm, fibrous, and did not stick to the fur, so differences in diet could have affected the likelihood that gorillas slept on their faeces (cf. Goodall & Groves, 1977; Dixson, 1981). Reynolds (1965) pointed out that chimpanzees, which are frugivorous, have soft faeces and are careful to deposit them outside the nest. I suggest that differences in aspects of the gorillas' defaecation at Lope were related to diet and dung consistency.

7. Day-Nests

The small number of day-nests found at Lope ($N = 24$) may have been partially due to a general difficulty locating nest-sites in this habitat, but it seemed that nests were not constructed during many rest periods. Day-nests were uncommon elsewhere: Merfield (1954) never saw a day-nest; Kawai & Misuhara (1959) guessed that nests were built during 30% of stops; and Schaller (1963:170) estimated 5% of rest-periods. Day-nests were simpler and less flattened than night-nests, as these nests were used for shorter

periods (Schaller, 1963:170). Several authors used a lack of dung with day-nests as a criterion to distinguish them from night-nests (Bolwig, 1959; Donisthorpe, 1958; Kawai & Misuhara, 1959; Osborn, 1963), but according to Schaller (1963:170) dung was present in small amounts. This was confirmed at Lope, where dung was found with 20.8% day-nests.

In some regions of East Africa gorillas built day-nests in trees (Blancou, 1955; Schaller, 1963:194). At Lope all day-nests were built on the ground, and the majority were herbaceous (87.5%). The other 12.5% (N = 3) were 'mixed'). On one occasion 3 rest-sites were found in the savannas, where areas up to 30 m in diameter had been trampled, and day-nests had been constructed from shrubs, ferns, and grasses (see Williamson et al, 1988).

D. DISCUSSION & CONCLUSIONS

The present study has demonstrated that the area of gorilla nest-sites at Lope was correlated with the number of nests present, and that these sites were smaller than those analysed by Casimir (1979) at Mt. Kahuzi. Nest materials reflected the structure and composition of the vegetation, and most differences between populations could be explained in these terms. Dung was flattened in only 1.5% nests, and this may have been related to the soft consistency of dung eliminated by the gorillas at Lope who ate large amounts of fruit. Only 37.3% of nests had overhead cover, but these formed a larger proportion of the sample than nests studied elsewhere. Tree-nests formed 11.8% of the sample, and most of these seemed to have been built by the smaller individuals. The maximum height at which nests were recorded was 16 m. Some seasonal trends were found in the gorillas' tendencies to nest in trees and to defaecate in their nests.

The possible benefits of nesting in trees should be considered, as a small proportion of gorillas do so. At Lope elephants were virtually absent during the dry season, but often encountered during the rainy season. Their presence coincided with a high proportion of gorillas' nests built in trees. Although this seasonal trend has been discussed in relation to dampness of the ground, the gorillas may also have been avoiding potential disturbance by elephants, which were active at night. However, such a hazard was not a

strong selective pressure, as the number of ground-nests was always high.

It has been suggested that gorillas were more inclined to nest in high trees in Cameroon, and at Utu in Zaire because of locally high hunting pressure (Critchley, 1968; Dixson, 1981), although I contend that gorillas in trees would be easier to spot, and more vulnerable as they could be more easily surrounded. Gorillas sleeping in trees may have been less vulnerable to other predators such as leopards (Pitman, 1935), which occurred at Lope, but which were not considered to pose a serious threat to the gorillas.

Variation in the frequency of nesting in trees is also related to environmental factors, such as the availability of suitable vegetation. For example, a tree trunk must not be too broad to climb, or else its branches must be accessible from the ground, either via a neighbouring tree or vines connected to the canopy; a suitable tree must have flexible branches which can be bent, leafy foliage to form a cushion, and must be strong enough to support the weight of an ape. The low incidence of tree-nesting in 2 populations of mountain gorillas was not considered to be due to limited site availability (Schaller (1963:181). Similarly, a lack of sites would not have accounted for the small number of tree-nests found at Lope. Differences between the heights of nests in 2 forested regions of Zaire were attributed to structure of the forest: more tree-nests were found in secondary and mixed forest with good access to the many strata, whereas in 'primary' forest many trees were too large to climb and were isolated from the shrub layer (Goodall, 1974:146). It seemed unlikely that trees at Lope were inaccessible. Herbaceous vegetation was abundant throughout most of the study-area (Rogers & Williamson, 1987), so the gorillas may simply have preferred to nest on the ground most of the time.

Another feature of the habitat which may have influenced the vertical distribution of nests was the variation in windspeed at different heights in the forest canopy. Windspeeds of 3 km/hr were reduced to 300 m/hr at 18 m, and 20 m/hr at 2 m in Gabonese forest (Barret & Lefeuvre, 1981, cited in Tutin & Fernandez, 1983a). Chimpanzees have been found to nest lower on windy evenings (Goodall, 1962; Reynolds, 1965). By choosing to sleep on the ground or at low levels gorillas may have avoided high winds for reasons of comfort or thermoregulation.

The apparent uniformity of nest-building across populations of gorillas suggests that

this behaviour is to some extent innate. Most investigations of the influences of 'nature' and 'nurture' on nest-building have involved captive chimpanzees, but it is reasonable to generalise from these studies, as the only major difference in the nesting patterns of great apes is in their vertical distribution. Studies of captive apes have suggested some stereotyped features of nest-building: when insufficient material was provided, chimpanzees arranged it in a circle around their bodies, but did not form a supportive structure (Kohler, 1927); a captive-born infant orang-utan presented with nest material displayed some of the action patterns of nest-building (Lethmate, 1977).

The importance of early experience was indicated by differences between wild-born and captive-born chimpanzees when provided with suitable materials: only the wild-born subjects built recognisable nests (Bernstein, 1962). This study also showed that age was a critical factor: juveniles' nests were often crude, but their motor patterns became more efficient with age, and all chimpanzees showed improvement when re-tested 7 years later. In another study of nest-building by chimpanzees, gorillas and orang-utans, Bernstein (1969) found no consistent differences between the construction techniques and the end products of each species. The immature gorillas all produced crude nests, but as age was a critical factor Berstein concluded that nest-building by all 3 species of apes was similar. Thus early experience is necessary for the development of nest-building. Infant gorillas build practice nests in the wild (Schaller, 1963:195; Fossey, 1979; present study) and the behaviour patterns required for nest-building could become coordinated during such activity.

Nest-building in the great apes seems to be innate, but refined by social learning. Nest-building occurs consistently both between and within species of great apes, so it is likely to have been retained from a common ancestor. This ancestor was probably arboreal (e.g. Susman, 1987). Terrestrial nesting may have become more prevalent as the body weight of gorillas increased and they became more terrestrial (e.g. Goodall, 1974:167; Dixson, 1981).

Schaller (1963:197) stated that the possible functions of many gorillas' nests were not evident, so why do gorillas build nests? A plausible explanation is that these beds provide comfort, and the significance of comfort may be inferred from seasonal differences

found in the proportion of tree-nests at Lope, which were presumably a means to avoid contact with wet ground. Nests were rarely constructed to provide shelter (cf. Pitman, 1935). Functions varied with the type of nest: ground-nests prevented direct contact with the soil; nesting above ground may have been a way to avoid damp ground, or to avoid nocturnal browsers, such as bushpigs, buffalo or elephants as stated above.

As for the absence of nest re-use, there are several possible reasons why new nests are produced each night: fresh nests may be softer, warmer and thus more comfortable than ones in which the leaves are already drying (Nissen, 1931). However the establishment of new nest-sites is likely to have been more important than the building of new nests *per se*. If predators had been a major factor, varying the location of sleeping-sites may have been advantageous (see Anderson, 1984). Also regular re-use of nest-sites would have led to an accumulation of faeces, the odour of which could have attracted predators. However, I have already dismissed predation as an important influence on the gorillas' nesting habits at Lope. Re-use of sites would also have increased the chances of reinfestation by internal parasites (Hausfater & Meade, 1982), and ectoparasites (MacKinnon, 1974). Merfield (1954) claimed that gorillas were free from ticks, although at Lope elephant ticks (Amblyomma tholloni) were occasionally identified in the gorillas' dung, which had presumably been ingested during grooming.

But the most important factor determining where gorillas spent the night was probably where they were feeding at the end of the day. Travelling through the home range may have required a substantial expenditure of energy. Gorillas nesting wherever they found themselves towards nightfall would not have had to make long return journeys to a particular site, and so would have avoided incurring a certain energetic cost, which would have been especially high for such a large bodied species. Goodall (1977) stated that eastern lowland gorillas nested wherever they were feeding near nightfall, using whatever vegetation was available in the immediate vicinity, a view shared by Schaller (1963). Bingham (1932) thought that selection of nest-sites by mountain gorillas was a matter of expediency, rather than foresight. There is no evidence to suggest that apes deliberately travel to certain areas solely to sleep. Forest primates in general seem to sleep in areas where they have been feeding in the late

afternoon (Anderson, 1984).

In conclusion, nests and nest-building seemed to be similar across all populations of gorillas. At Lope variation was expressed in the proportions of exposed nests and of nests built in trees. Previous studies have concluded that most variation was caused by features of the environment, such as structure of the vegetation, the climate, and the seasonal abundance of nocturnal intruders (e.g. Goodall, 1974; Schaller, 1963). This view has been supported by the present study.

CHAPTER 6: SOCIOECOLOGY

A. INTRODUCTION

This chapter deals with the gorillas' daily and seasonal travel patterns and habitat use, and some aspects of their social behaviour. The data are mainly descriptive, and amenable to few statistical analyses, but so little is known about western gorillas at present that this information is of value. The data were collected during 162 contacts totalling 138 hrs (median = 23 mins, R = <1-370 mins), with 28 hrs observation (median = 5 mins, R = <1-181 mins, N = 116).

B. DIURNAL ACTIVITY

The daily activity patterns of gorillas at Lope seemed to be broadly similar to those of mountain gorillas. Gorillas at Lope probably left their nests at dawn, as described for other populations (e.g. Blancou, 1955; Schaller, 1963:139; Groves & Sabater Pi, 1985). One group was feeding close to the nest-site when contacted at 06.20 hr. One adult female stayed in her tree-nest until 08.10 hr, although the rest of the group were already foraging.

Part of each day was spent feeding on THV, the herbaceous Aframomum and Marantaceae which formed the gorillas' staple diet. Generally each day started with an intensive feeding bout, indicated by piles of split Aframomum stems and the trampling of vegetation in the vicinity of the nest-site. Schaller (1963:139) noted that gorillas fed for about 2 hours on rising, until they became satiated. Examples of a day's activities are illustrated in Figure 6.1.

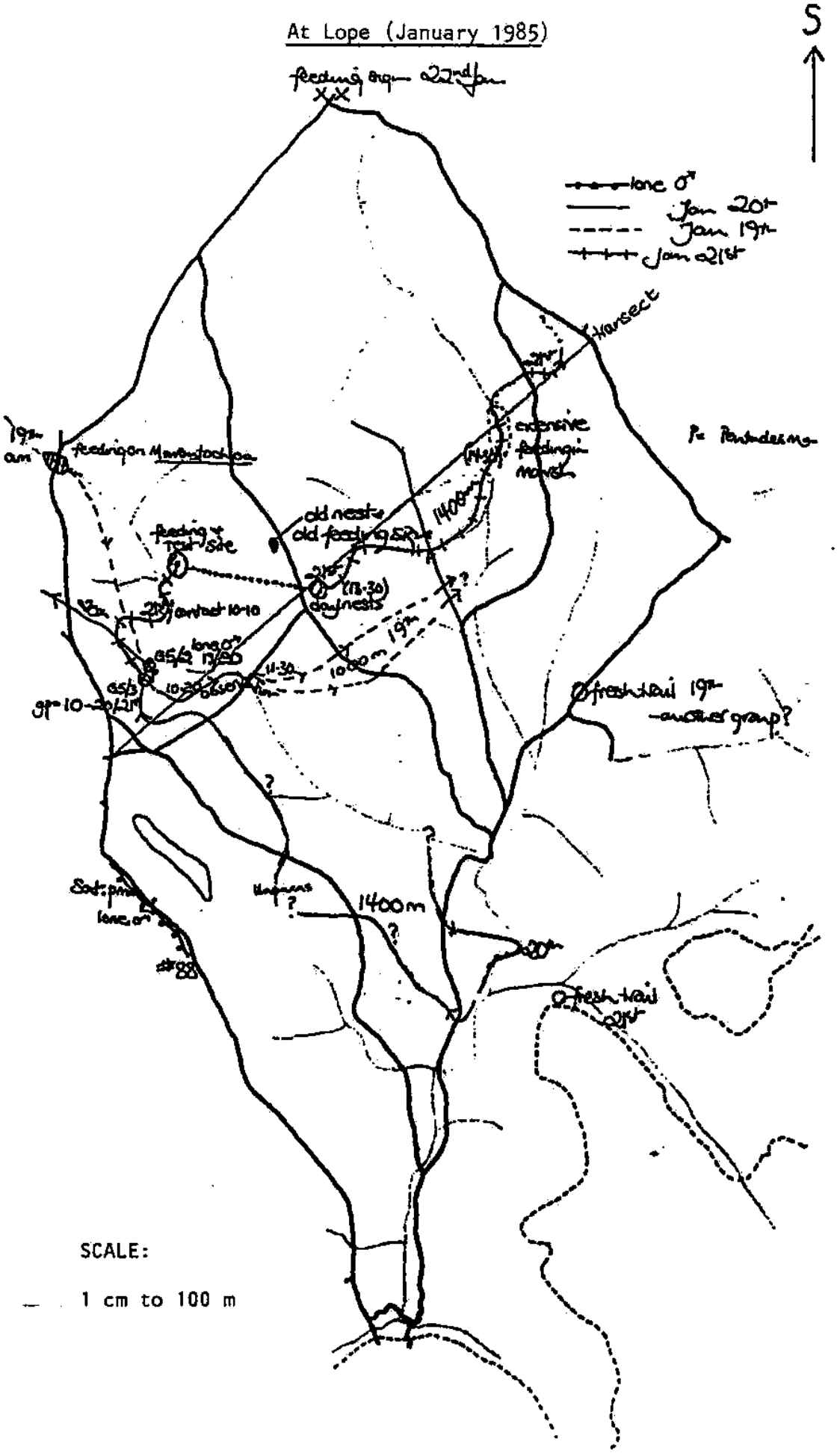
The gorillas' activities determined the speed with which they moved through the habitat. Three rates of travel were discriminated.

(i) SLOW: intense foraging on THV, so movements were slow, e.g. 30 m/hr, 70 m/hr, 100 m/hr;

(ii) TRAVEL-FEED: gorillas chose to eat less THV, or the density of THV was reduced, thus movements were unhurried, but faster than when browsing, e.g. 500 m/hr;

(iii) RAPID TRAVEL: moved purposefully from one area of forest to another between

Figure 6.1 An Example of the Daily Movements of Gorillas At Lope (January 1985)



fruit sources, or fleeing from an observer, e.g. 550 m/hr, 625 m/hr, 1200 m/hr, 1400 m/hr.

The regularity of the gorillas' mid-day rest periods was not established. Day-nests were built 200 m from night-nests on 2 occasions, and 600 m on another. One lone male was heard snoring while resting between 11.20 hr and 12.35 hr. At Kabara a long feeding period in the morning was followed by a rest period somewhere between 10.00 hr and 14.00 hr, and the afternoon was spent foraging and travelling until nests were constructed at about 18.00 hr (Schaller, 1963:146). Gorillas were rarely active at night: once chest-beats were heard between 19.10 hr and 19.50 hr from a group nesting close to the forest edge at Lope. Schaller (1963:148) reported that silverbacks chest-beat intermittently through the night if other gorillas were nearby, and Jones and Sabater Pi (1971) heard chest-beats until 20.00 hr.

C. RANGING

The gorillas' movements were drawn onto maps of scale 1:10000, and distances travelled were measured from these maps. No corrections were made for topographical variation, though the study area was relatively flat. Trails were often winding or circuitous, but small deviations were not shown on the maps. Nor were individual detours from principal routes taken into account, so distances were consistently underestimated. Where trails were patchy and feeding remains dispersed, it was assumed that gorillas had moved in relatively straight lines, representing the minimum distances travelled. Feeding remnants separated by more than 50 m were drawn on the maps as broken trails and not measured.

To estimate distances travelled during 24 hour periods required the location of consecutive nest-sites and the routes travelled between them. At Lope it was rarely possible for us to back-track complete journeys; feeding remains on trails were identifiable for several days, but the gorillas did not feed continously, and entire day journeys were established only twice. The majority of the records on group movements were incomplete, and many of the data relate to distances travelled, with little information about the time involved.

1. Day Journeys

Variable distances were covered during the early part of the day: by 10.00 hr groups moved between 100 m and 600 m from nest-sites, one group had travelled over 250 m and rested by 08.40 hr. Shorter distances were recorded when large amounts of THV were ingested, and progression was slow. Many trails could not be traced back to nest-sites, but journeys made by known times included over 900 m covered by 12.40 hr, and over 550 m by 13.30 hr. Distances travelled between rising and early afternoon included 1000 m by 13.20 hr, and 1400 m by 14.00 hr.

The longest journey recorded was 1800 m. The maximum route-lengths tracked (see Appendix 6.1 and Table 7.1) exceeded 1 km in 5 out of 12 months, although 6 of these values represented only half days. Many short trails of 100 m to 300 m were recorded each month, but the proportion of each day journey these distances represented was unknown. Complete records were available for only 2 days, when groups travelled 320 m and 800 m. I have focused on the longest trails, as indicators of the influence exerted by widely dispersed trees on the gorillas' ranging patterns. Large distances were consistently recorded during 2 months when gorillas were visiting gallery forests in search of Uapaca fruits: one group travelled over 1550 m, 1450 m and 1110 m on 3 consecutive days in December 1984, and distances of 1000 m, 1400 m, and 1700 m were measured during January 1985.

The density of food remains, and hence the conspicuousness of trails was related to food-type and distribution: if ground vegetation was relatively sparse the gorillas could eat little, and so left few indicators of their travel routes. If they fed intensely, food remains were close together and the trails were much clearer. Also, when succulent fruits were abundant, gorillas moved fairly rapidly between sources, consuming little THV, and so left few signs of their presence, so that trails once lost were difficult to relocate. Thus slow moving gorillas, covering shorter distances, were tracked more successfully than those travelling quickly and widely in search of fruit. Therefore, large recorded distances did not neccesarily imply that the gorillas had *travelled* further, but that we had been better able to follow their routes.

Although two extreme foraging strategies have been described, this distinction was

rarely clear cut, as fruit and THV were of varying importance each month. Also, even when fruit abundance was low gorillas, still travelled between trees producing new leaves. The maximum journey length recorded was 1800 m, when a group fed on the flushing leaves of Chlorophora excelsa trees, which had a mean density of <1 per hectare.

The spatial distribution of fruiting trees differed between seasons. For example, the species sought during the first 3 months of 1984, Celtis tessmannii, Heisteria parvifolia, Santiria trimera, and Zanha golungensis, were widely separated, and 3 of these species occurred in clumps. It was necessary for gorillas to travel 200 m to 400 m between clumps, as the total density of trees was only 5 per hectare. When Cola lizae fruits were a major dietary item in April and May 1984, the high density of Cola trees (100/ha, 20 'adult' trees/ha) meant that sources were close together, and the gorillas concentrated their activities in certain areas.

Shorter distances were travelled as the gorillas' diet shifted from fruit to THV, but the maximum length of trail mapped each month did not correlate with fruit abundance ($r(9)=.3119$, $p=.414$). One overiding factor affected these data: our ability to track the gorillas. As explained above, gorillas moving rapidly were difficult to follow, and we lost their trails, so only partial day journeys were recorded. Also as the study progressed we learned routes which the gorillas used regularly, became more familiar with the forest in general, became more proficient at spotting feeding signs, and predicting the routes gorillas had taken. Thus we were more successful at catching up with, or in planning to intercept the gorillas. The increase in our proficiency is borne out by a weak correlation between the number of trails found per field-day and the number of months into the study. Trails were followed for greater distances as the study progressed ($r(16)=.548$, $p=.028$).

Gorillas covered 700 m in 30 mins, 800 m in 4 hr 50 mins, and so on, thus it seems likely that they travelled greater distances during an entire day's ranging than those measured. Also, there may have been a bias in the data, as Schaller (1963:137) found that mountain gorillas travelled further during the afternoon, but at Lope more trails were found in the mornings (see Appendix 6.1), so the distances moved during half a day were perhaps less than half the total day-journey length. Tutin (pers.comm.) has tracked

gorillas at Lope for 3.5 to 4 km during days when they have been feeding at widely dispersed fruit sources. At this point it is possible to conclude only that the gorillas at Lope travelled relatively large distances each day, often exceeding 1 km. Also, gorillas seemed to travel less when fruit was scarce, feeding instead on widely available herbs. Similarly, chimpanzees and orang-utans travelled less when food was scarce (Wrangham, 1979; Galdikas, 1979).

Table 6.1 presents comparative data on the day journeys of gorillas and chimpanzees. Mountain gorillas usually travelled less than 0.5 km per day, eastern lowland gorillas ranged slightly further: 600-1100 m, and western gorillas in Equatorial Guinea covered 1 km daily. Clutton-Brock and Harvey (1977a) demonstrated that the degrees of frugivory and terrestriality influenced day ranges. On this basis the frugivorous western gorillas would be expected to travel further during a day than the herbivorous mountain gorillas, as the distribution of food trees in tropical forest dictated that the gorillas travel further between sources.

The diet of gorillas at Lope was closer to that of sympatric monkeys than to that of eastern gorillas (Chapter 4), although from the relationship which exists between body weight and ranging (e.g. Milton & May, 1976) gorillas would be predicted to range further than the smaller frugivorous, arboreal monkeys, for example, mangabeys (1127m, Waser & Floody, 1974), or crowned guenons (1500-2000 m, Gautier-Hion, 1978).

The mean day journeys of lowland gorillas may be similar to those estimated for chimpanzees (e.g. 2.6 km, Pierce, 1978; 3.9 km, Wrangham, 1975), and bonobos (2.4 km, Kano & Mulavwa, 1984). Gorillas are closer in body weight to chimpanzees and bonobos than to monkeys, but group size also influences ranging, and both chimpanzee species travel in parties both smaller and larger in size than gorilla groups (see Wrangham, 1986). Although the data available are incomplete, the present study points towards day-journey lengths of between 1 km and 4 km for lowland gorillas, depending on the abundance and distribution of fruit sources. This is congruent with expectations for a large, terrestrial, frugivorous primate.

Table 6.1 Day-Journey Lengths of African Apes Recorded at Various Study-Sites

STUDY	DAY-RANGE ESTIMATES/m	
	Mean	Range
Mountain Gorillas		
Schaller (1963)	337-663	100-1800
Caro (1976)		365, 460 *
Elliot (1976)	522	83-1342
Fossey & Harcourt (1977)	350-450	100-2500
Yamagiwa (1986)	434	28-1671 *
Eastern Lowland Gorillas		
Casimir & Butenandt (1973)	900	600-1100
Goodall (1977)		140-3400
Western Lowland Gorillas		
Jones & Sabater Pi (1971)	900, 1130	700-1600
Chimpanzees		
Pierce (1978)	2400 (median)	
Wrangham (1975)	3900	
Bonobos		
Kano & Mulavwa (1984)	2400	400-6000

* lone males

2. Home Ranges

A system of grid-squares, 200 m x 200 m, was imposed on a map of the study-area, onto which all trails and contacts confirmed to have been with 1 of 4 particular groups were marked. At least 3 other groups were contacted less frequently, and usually at the periphery of the study-area. Data from 61.1% of contacts when groups were not identified were excluded, as were contacts with lone males (13.0%), and other known groups (10.5%). Therefore only 15.4% (x = 25) contacts were included, but 49.7% (x = 56) nest-sites. The data for Groups 2, 3, 4, and 5 were collected during only 12, 7, 4, and 8 months respectively, with an average of 1.5 contacts per group per month. Hence, ranging data for each group were sparse. They were also highly variable: Group 3 was recorded in 36 grid-squares in 7 months, whereas Group 4 entered 37 in only 4 months. Predictions based on this limited information would be unreliable. Criticisms have been aimed at estimates of home ranges extrapolated from more complete data than those presented here (e.g. Fossey & Harcourt, 1977), and sampling errors related to the size of grid selected can lead to large underestimates of the actual area of habitat used (Olsen, 1986). In addition, no correction was made for parts of the Lope study-area which we did not search during any particular month, thus I have made no attempt to define a typical annual range for this population.

Comparative data, given in Table 6.2, show that mountain gorillas' home ranges are usually 8-9 km^2, although eastern lowland gorillas may have ranges of over 30 km^2. Again predictions can be made from the general trends observed among different species of primate. Home-range size is affected by body size, group size, and diet (e.g. Milton & May, 1976; Clutton-Brock & Harvey, 1979). These factors, together with features of the habitat such as food density, determine the area neccesary to supply a group with an enough food to meet their nutritional requirements. The frugivorous habit of western gorillas in tropical forest dictate that they range large distances in search of fruit, not only on a day to day basis, but throughout the year.

Chimpanzees and bonobos in tropical forest provide useful reference points, with respective estimated home ranges of 23 to 38 km^2 (e.g. Ghiglieri, 1984a), and 22 km^2 to 58 km^2 (Badrian & Badrian, 1984; Kano & Mulavwa, 1984). However these are the ranges

Table 6.2 Home Ranges of African Apes at Various Sites

STUDY	HOME-RANGE ESTIMATES/km2
Mountain Gorillas	
Schaller (1963)	10.4-22.0 *
Fossey (1974)	8.0
Fossey & Harcourt (1977)	4.0-8.1
Vedder (1984)	8.6
Watts (1983)	9.0
Yamagiwa (1987)	9.7
Eastern Lowland Gorillas	
Casimir (1975)	31.0
Goodall (1977)	16.0-34.0
Western Lowland Gorillas	
Jones & Sabater Pi (1971)	5.5, 6.8
Chimpanzees	
Pierce (1978)	15.0 (Kasekela), 3.9 (Kahama)
Wrangham (1975)	12.0
Nishida (1979)	10.4 (K group), 13.4 (M group)
Ghiglieri (1984a)	23.1-37.9
Boesch & Boesch (1984)	27.0
Bonobos	
Badrain & Badrian (1984)	22.0
Kano & Mulavwa (1984)	58.0

* over-estimated according to Goodall (1974)

of communities numbering more than 50 individuals, and are thus about 5 times larger than groups of gorillas. Western gorillas in mature forest are likely to have home ranges which are smaller than those of chimpanzees, but larger than those of mountain gorillas.

One aspect of the gorillas' ranging indicated by the data from Lope was the extent of overlap between different groups. This has been underestimated as contacts with unidentified groups were excluded, and much of Group 5's range was not included, but their excursions into the demarcated area overlapped with Groups 2, 3, and 4 by 20.0%. A 35.3% overlap with other groups was recorded for Group 2, while Groups 3 and 4 shared over 40% of their ranges (41.7% and 43.2%). There is no evidence that eastern lowland gorillas defend their ranges (Casimir & Butenandt, 1973), and Goodall (1977) estimated that their home ranges overlapped by 40-50%.

Whether or not groups of gorillas use the same areas at the same time is critical for an assessment of potential resource competition. Some instances of groups using the same areas within a few days of each other were noted at Lope.

3. Use Of The Habitat

The gorillas wandered throughout the forest at Lope and fed in all vegetation types, except sedge marshes. Marantochloa marshes were used extensively, as were streams, where these herbs grew in monospecific stands. One group foraged in 3 separate streams during a single day. Groups sometimes divided and foraged on THV along the opposite banks of streams for 100 m or more.

Although gorillas used paths worn by large mammals, they also moved through thick THV, made 'tunnels' under particularly dense patches, and crossed steep rocky slopes with no apparent difficulty. They foraged for 500 m or so, parallel to old logging roads where Aframomum grew in abundance, and groups split to feed on either side of roads before rejoining. Two groups even browsed beside a road used regularly by vehicles.

Several seasonal ranging patterns were detected. In May 1984 groups ranged in small areas, feeding primarily in the high density Cola lizae trees. One group foraged

on a single ridge for almost 2 weeks; another spent 4 days feeding within an area of 300 m radius. While Dialium sp. was an important food in June and July 1984, one area where Dialium trees were especially common was used heavily by gorillas, chimpanzees, and hornbills. From October to January gorillas were attracted to the gallery forests by fruiting Uapaca guineensis trees, which were rare in the main forest block (see below).

Gorillas were inclined to re-use the same routes when passing through particular areas, and to revisit fruiting trees for several consecutive days when these trees occurred at low densities, usually until the crops were exhausted. The areas around such trees became riddled with fresh, recent, and old trails, often confused with elephants' trails. Examples of re-use included: a solitary male who fed and nested within a 200 m radius of three Detarium macrocarpum trees during a 10-day period in August 1984; a Pseudospondias longifolia tree revisited several times by gorillas, chimpanzees, and elephants when other fruits were scarce in September 1984; and a Pentadesma butyracea tree which was returned to repeatedly in February 1985. Small trees were not revisited as gorillas tended to consume their crops at one sitting.

When fruit was scarce the gorillas meandered throughout the forest, rather than using particular areas. No single areas were favoured by individual groups in August 1984, January, March, and April 1985, except that during those months greater use was made of the forest fringes.

4. Streams & Savannas

The study-site at Lope is bordered by savannas, providing a sharp contrast in habitats, and two interesting aspects of the gorillas' behaviour were their use of these open spaces and of water.

a) Streams.

It has been thought that gorillas avoid entering water whenever possible, and cross streams only where there are natural bridges (e.g. Schaller, 1963:298). At Lope gorillas walked through streams, even when log bridges were available, except after heavy rain when the water rose by up to 1 m. Juveniles were seen walking through water bipedally;

infants rode on their mother's backs; a play-chase between juveniles ended up in a stream; day-nests were found on a half-submerged log; a lone male walked through 40 m of fast-flowing water 25-30 cm deep; and groups foraged in streams and marshes.

Knuckle-prints in the sandy 'beaches' either side of streams were useful indicators of the gorillas' movements, although in the dry season some beaches became too cluttered for individual trails to be distinguished. Moving through the forest necessitated passing through or over some of the numerous streams, particularly after heavy rain. Perhaps as a result of this, the gorillas seemed not to fear water, as is true of many gorillas in captivity (e.g. Golding, 1972; Cousins, 1978).

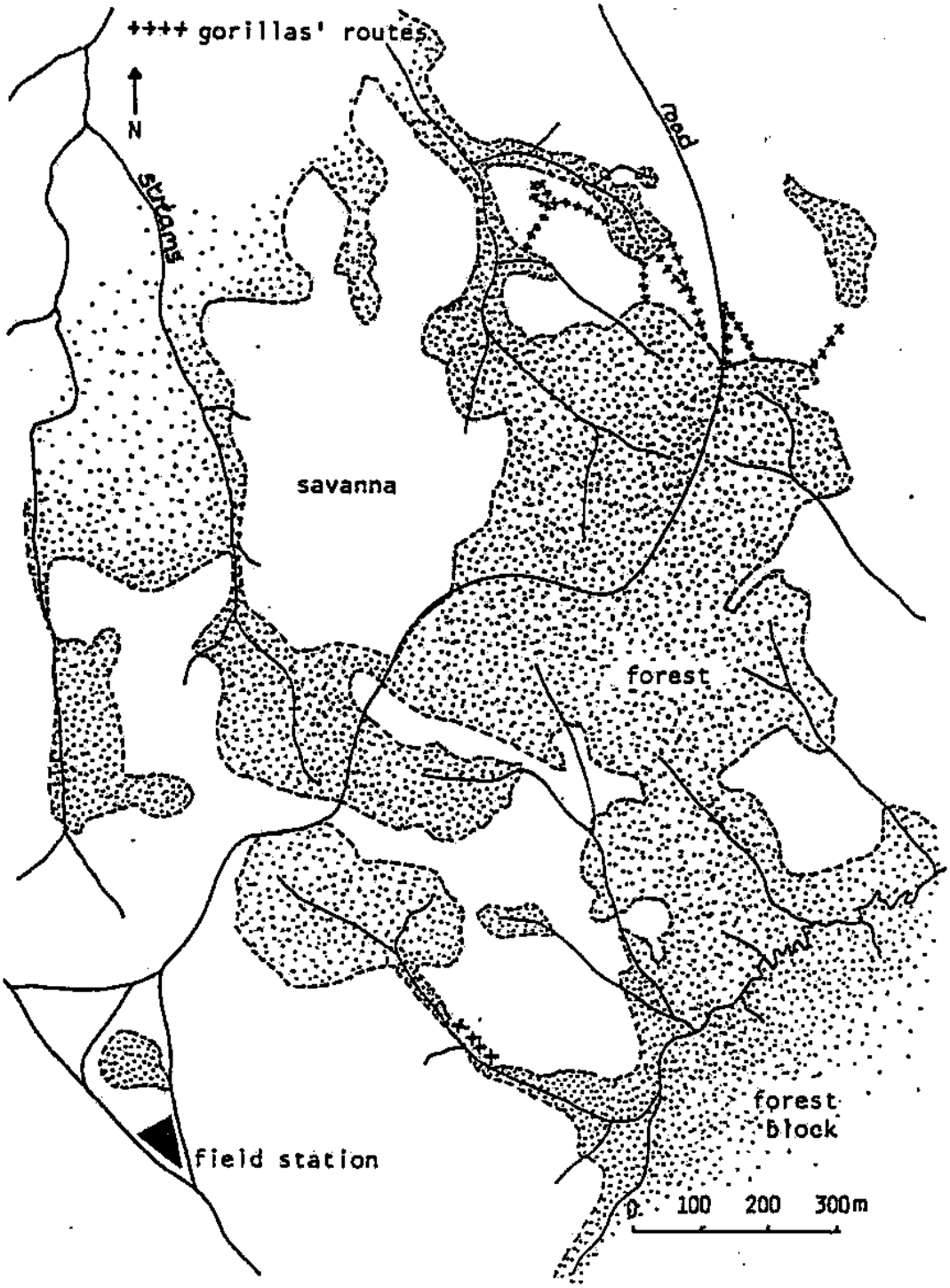
b) Savannas.

A network of gallery forests crossing the savannas at Lope provided a seasonal attraction in the form of Uapaca fruits. Groups and solitary males crossed 50 m to 250 m of open savanna during October and January, when travelling to and from the galleries (Figure 6.2). Three rest-sites up to 30 m in diameter were found, and one group even built day-nests in the savanna (see Williamson et al, 1988). In April and May 1985 gorillas fed in an isolated mango tree, Mangifera indica, over 1 km from the main forest block. However, groups clung to the forest edges where possible, and acted cautiously without the cover of vegetation. Such behaviour may be poorly known rather than unusual among western gorillas, as Malbrant and Maclatchy (1949:63) also noted that gorillas in Gabon traversed savannas and gallery forests, and in Cameroon gorillas crossed grassland slopes to forested valleys (Critchley, 1968).

D. CLIMBING

The arboreal feeding of gorillas was discussed in Chapter 4. Although gorillas moved slowly and with caution in trees, they were confident enough to perform non-feeding activities in trees: all age-sex classes rested supine on branches 10 m or more above ground; one adult female rested on a small branch with her feet placed against the trunk; and a female spent 30 mins grooming her infant while sitting at the top of a tree with her back against the trunk. Despite loud cracking and splintering noises, a silverback 15 m above ground fed at the ends of narrow branches for 15 mins.

Figure 6.2 Some of the Routes Used By Gorillas Travelling To and From the Gallery Forests at Lope



Gorillas walked quadrupedally along branches, and descended feet first, moved slowly, unless startled, in which case they slid rapidly down trunks, sometimes jumping the last 2 m to the ground. When ascending and descending large trunks, many individuals transferred to smaller trees or saplings, or used lianes or vine towers to reach the ground. Juveniles sometimes transferred at heights of 18-20 m by swaying branches of the canopy until they could reach a neighbouring tree. Immatures also showed a tendency to play in trees while feeding, hanging from one limb, for example.

Mothers carried their infants while climbing, but even normally ventrally-riding infants moved independently on branches, remaining within arm's reach. Infants slid round from a dorsal position to rest between their mother's thighs while she sat down to browse.

Mountain gorillas spend little time above ground. Schaller (1963:87) stated that mountain gorillas were excellent climbers, but only 2.9% of their daily activity takes place in trees (Tuttle & Watts, 1985). Gorillas start climbing at 6-12 months of age (Fossey, 1979), and are keen climbers in captivity if given the chance (e.g. Hancocks, 1983 Yerkes & Yerkes, 1929:408). Eastern lowland gorillas climbed more than mountain gorillas; the forest at Mt. Kahuzi offered a more 3-dimensional habitat and a wider variety of levels for exploitation (Goodall & Groves, 1977). Similarly there were more levels to exploit in the forest at Lope, than in the comparatively open vegetation of the Virunga Volcanoes. Gorillas are modified brachiators (Napier, 1963), and at Lope both juveniles and adults were seen to locomote in this manner.

E. SOCIAL BEHAVIOUR

The social structure of gorillas at Lope resembled that of mountain gorillas, that is, they lived in stable family groups (median size = 10, N = 8), each led by an adult silverback male (one group contained 2 silverbacks). Some silverbacks were solitary, as in the eastern populations (e.g. Schaller, 1963:121; Yamagiwa, 1986). The composition of the 4 main groups studied was:

GROUP 2 (*Southern Group*): 1 silverback, 2 adult females, 1 subadult female, 2 infants, N = 6;

GROUP 3 (*Monte Cristo*): 1 silverback, 3 unsexed adults, 1 adult female, 4 juveniles, 1 infant, N = 10+;

GROUP 4 (*Victor Hugo*): 1 silverback, 4 unsexed adults, 5 adult females, 5 juveniles, 1 infant, N = 16+;

GROUP 5 (*St. Exupery*): 1 silverback, 1 unsexed adult, 5 adult females, 2 juveniles, 1 infant, N = 10+.

Researchers at Lope saw few social interactions between gorillas. Twice juveniles were believed to have sought reassurance from adults when crossing open spaces. The only grooming seen was that of an infant by its mother. Juveniles' play sessions involved charging, slapping, thumping, and chest-beating, which lasted for up to 45 mins. Juveniles and infants dangled in trees and swatted each other, and several instances of solitary play were seen, such as plucking leaves, putting them in the mouth, then placing them between the toes. Apart from these few anecdotes, most of the information obtained related to intergroup or interspecific interactions.

1. Communication

a) Vocalisations.

Vocalisations were categorised from Fossey's descriptions (1972). Hoot barks and hiccup barks were not differentiated from question barks, as they are intergraded (e.g. Marler, 1976). Sounds are degraded by reverberation in tropical forest (Waser & Brown, 1986), so subtle distinctions were more difficult to make. Soft grunts and belches probably helped to maintain contact between group members in dense vegetation where visibility was considerably reduced, although it has been suggested that these low sounds are also associated with competition (Harcourt *et al*, 1986). Low rumblings were heard as groups left rest-sites; bark-like grunts came from a group following a silverback; travelling groups emitted soft low coughs; and twice silverbacks "whinnied" during rapid travel. Many sounds were produced in contexts unknown to us, although others were elicited by the presence of another group, or an observer. These included threat barks and roars during aggressive displays, question barks, screams, squeals, and coughs. The gorillas' vocal repertoire and production was dominated by the silverbacks. Mountain

gorilla silverbacks gave 92% of all vocalisations emitted by groups (Marler & Tenaza, 1977).

b) Chest-Beating.

Only infant gorillas did not beat their chests. Juveniles chest-beat in play and during contacts with human observers. The median number of beats per series for juveniles was 4 (N = 32, R = 2-6), slightly less than the 5 for adults (N = 26, R = 2-10). Females' and juveniles' chest-beats lacked the resonance of the adult males' "pok-pok" due to anatomical differences (Schaller, 1963:225). Chest-beating may have several functions, for example in intergroup communication and intimidation, although it may be provoked in any 'exciting' situation (Schaller, 1963:233; Dixson, 1981:130). One solitary male chest-beat for 70 mins at mid-day before falling asleep, when no other gorillas seemed to be within hearing range.

2. Intergroup Interactions

Two groups were detected within auditory range of each other five times; three of these were in one area during the same month. This area may have been at the perimeter of either groups' home range, or the gorillas may have been using the same food sources, plant species with limited dispersal. Sometimes roars from distant groups seemed to be ignored, at other times groups exchanged chest-beats and vocalisations for up to 45 mins. One group approached another to 150 m, after chest-beating and roaring at each other from 200-300 m. The second group retreated after further displays were heard. This contact lasted 2 hrs 15 mins. Following two intergroup interactions large quantities of diarrhoeic dung indicated that the gorillas had probably been stressed, although no physical contact seemed to have occurred.

Solitary males were seen within 200 m of groups, and no reaction was detected from either party. One lone silverback seemed to follow the fresh trail of a group, which may indicate that the relationships between lone males and groups resemble those found in mountain gorilla populations, where the ranging of lone males is largely influenced by the movements of groups (Yamagiwa, 1986).

3. Interspecific Interactions

The gorillas' responses to human observers will be described in Chapter 7. Judging by trail evidence, gorillas and their most important competitors (in terms of dietary overlap and biomass) the elephants and other primates, came close together many times. Feeding competition among frugivores was discussed in Chapter 4, but chimpanzees, monkeys, and elephants are considered again below.

a) Chimpanzees.

Gorillas and chimpanzees were observed during the same day on 10 occasions, sometimes within the same hour, but they showed no awareness of each other. Both species were known to be within the others' auditory range 17 times, including 6 gorilla-contacts, during which chimpanzees' pant-hoots were heard, with no apparent reaction from the gorillas. Garner (1920) remarked that the apes appeared to fear each other and avoid meeting, and Jones and Sabater Pi (1971) stated that they moved off in opposite directions. Cousins (1982) quoted a report suggesting that gorillas in Gabon gave way to chimpanzees when competing over fruit sources, although in Nigeria chimpanzees "seemed to stand in no fear of the gorillas, but were mixed with the band, and playing with the young ones" (Allen, 1931:9). In reality, however, the outcome of encounters between the two species of apes seems to depend upon the size and composition of their respective groups (Tutin & Fernandez, 1987a).

b) Monkeys.

No direct contacts were seen between gorillas and any of the 6 species of diurnal monkey. A group of black colobus once passed directly overhead without any attention being paid to them; spot-nosed guenons and gorillas fed in the same tree and ignored each other. Mangabeys sometimes responded to gorillas' displays by calling in alarm. No interactions between gorillas and monkeys were observed by Jones and Sabater Pi (1971), or by Schaller (1963:305), and it seems that there is little direct conflict between species of primates.

c) Elephants.

Elephants were present at high densities, particularly during the wet seasons. Three times when elephants were seen near gorillas, both parties ignored each other. Gorillas

approached a group of elephants only once, emitting "hoo" vocalisations and displaying, causing the elephants to flee. Merfield and Miller (1956, cited in Schaller, 1963:301) reported that a roaring male stampeded a group of elephants. Both Schaller (1963:301) and Fossey (1974) stated that gorillas avoided areas which had recently been trampled by elephants or buffalo.

F. DISCUSSION & CONCLUSIONS

Food distribution and abundance are known to have a strong influence on the ranging patterns of primates (e.g. Struhsaker, 1978; Raemaekers, 1980; Harrison, 1983; Kitamura, 1983; Waser, 1975). Blancou (1955) noted that certain areas of Gabon and Congo 'teemed' with gorillas during the dry season, when limited food supplies were concentrated in particular areas, and Sabater Pi (1966) suggested that the distribution of fruiting trees affected the movements of gorillas in Equatorial Guinea. The ranging of gorillas at Lope was clearly influenced by the seasonal availability of particular food-species: when fruit was abundant gorillas travelled widely between sources, but during periods of fruit scarcity they adopted a low-cost strategy, shifting their diet towards more abundant, but poorer quality foods, and travelling less.

Even in montane habitats, where food was abundant and seemingly unlimited, food quality and availability influenced the ranging patterns of eastern gorillas (Casimir & Butenandt, 1973; Caro, 1976; Goodall, 1977; Watts, 1983; Vedder, 1984). The day journeys of eastern lowland gorillas increased in length when Myrianthus holstii fruit was in season (Goodall, 1977).

Social factors also influence the ranging of gorillas (Fossey, 1974; Yamagiwa, 1987). The presence of other gorilla groups, or parties of chimpanzees may have had a major effect on the movements of gorillas at Lope, particularly as there seemed to be no distinct ecological separation of the apes. Jones and Sabater Pi (1971) proposed that resource partitioning between gorillas and chimpanzees in Equatorial Guinea was achieved temporally (seasonal segregation of habitat use), vertically (chimpanzees being arboreal, while gorillas remained on the ground), and by food selection (differing dietary specialisations). At Lope none of these strategies was in evidence. During the

present study it became clear that the feeding ecology of sympatric gorillas and chimpanzees was very similar, that they used the same areas of the habitat, and even fed in the same fruit trees, thus direct competition was likely. During periods of fruit scarcity the level of interspecific competition was mitigated by shifts in the gorillas' diets.

One interesting aspect of the social structure of gorillas at Lope is their group size in comparison to other populations. Two of the major constraints on group size are resource density and competition (e.g. Wrangham, 1979). At Lope fruits formed a major portion of the diet, and as the density of fruit sources was low, the level of competition between and within groups would have been more severe than among mountain gorillas, whose herbaceous foods occur at high density. Wrangham (1979) predicted that groups of gorillas living in lowland forests would be smaller than groups of mountain gorillas. This seems to have been supported by a paper by Harcourt *et al* (1981), which claimed that West African gorilla groups are smaller than East African groups. This conclusion was based on data from Equatorial Guinea with a maximum group size of only 12 individuals. However there have been several reports of large groups from West Africa, including Cameroon (N = 20, Ischac, 1938), Gabon (N = 19, Tutin & Fernandez, 1984), and Congo (N = 30, Blancou, 1955). With the exception of Tutin and Fernandez' study, these and most other reports of very large groups are dated (e.g. Derscheid, 1927; Schaller, 1963).

Table 6.3 compares group sizes recorded in East and West Africa. Only tentative conclusions can be drawn from the Lope data, as the sample is very limited (N = 8 groups), but the groups at Lope seem to be no smaller than those found elswhere, and the median group size of 10 nest-building individuals was twice that reported for other West African populations (Jones & Sabater Pi, 1971; Tutin & Fernandez, 1984), and by Harcourt *et al* (1981). Group size in East Africa is more variable (2-37), and although two groups consisting of at least 16 individuals were encountered during the present study, no really big groups were found, such as those of 42 at Mt. Kahuzi (Yamagiwa, 1983).

Ecological correlates for differences in group size are speculative (Harcourt *et al*, 1981), but in Cameroon the small size of gorilla groups was attributed to hunting pressure

Table 6.3 Comparative Group Sizes of Gorillas Recorded at Sites in East and West Africa

STUDY	MEDIAN GROUP SIZE	RANGE	N
East Africa			
Virunga Volcanoes only *	6	2-21	31
including Virungas' population *	9	2-37	64
excluding Virungas' population *	11	3-37	33
West Africa			
Equatorial Guinea *	5	2-12	29
Gabon (Tutin & Fernandez, 1984)	4	2-19	136
Gabon (present study)	10	4-16	8

* data from Harcourt et al (1981)

and habitat loss (Critchley, 1968), and groups of gorillas in the Virungas became smaller due to a reduction in resources per head of the population (Weber & Vedder, 1983). Similar pressures appear to have resulted in a reverse trend in some areas of Rwanda (Aveling & Aveling, 1987), and at Kahuzi-Biega, where groups of eastern lowland gorillas became very large as hunting pressure has increased (Goodall, 1974:35). The group size of gorillas at Lope will be discussed further in Chapter 8.

Three major points have arisen from the above comparisons of lowland and mountain gorillas. First, lowland gorillas' home ranges were almost certainly larger; second, lowland gorillas spent considerably more time in trees performing various activities, but mostly feeding; third, the social structure of gorillas seemed to be remarkably similar throughout the gorillas' range.

new data on time spent feeding by mountain gorillas (see Harcourt & Stewart, 1984). Given the apparent fragility of this relationship, data from western lowland gorillas, once they are available, may have a strong effect on similar correlations.

Gorilla gorilla beringei diverges from other primates on regression lines of home-range size and proportions of fruit/foliage in the diet (Harvey & Clutton-Brock, 1981). However, data from the lowland gorillas at Lope would likely fit with those for chimpanzees and bonobos.

The findings of the present study, in particular that the gorillas at Lope are largely frugivorous, have several implications for the gorillas' socioecology. I shall attempt to put the data into perspective, starting with an examination of anatomy, which may provide evidence for dietary specialisation. Dental morphology, anatomy of the digestive tract, and body size have all been used as predictors of the feeding behaviour of primates (see Garber, 1987), and I shall assess how they reflect dietary specialisations in lowland gorillas.

Comparisons are made between the gorillas at Lope, mountain gorillas which are folivorous, and the other species of great apes, which are described as frugivores (see Ghiglieri, 1987; Wrangham, 1986).

B. MORPHOLOGY

1. The Skull

In some aspects of their skull morphology lowland gorillas and chimpanzees are very similar: Shea (1983) found no significant 'reorganisation' of the facial complex of Gorilla g. gorilla and Pan t. troglodytes, as would have been predicted from differences found between Cebus capucinus and C.apella (Kinzey, 1974). He stated that "the primary facial shape changes distinguishing gorillas from chimpanzees are the same...as those distinguishing P.paniscus from P.troglodytes, or males from females within each of the three ape species, where no significant dietary differences exist" (Shea, 1983:59).

Differences in other aspects of skull morphology, namely the crania and mandibles, have been found within the subspecies of Gorilla and attributed to their ecological

diversity (Groves, 1967, see below).

2. Dentition

Comparing the 3 subspecies of Gorilla, Groves (1970b) noted that the teeth of Gorilla g. beringei were the largest, that jaw musculature was most developed in Gorilla g. gorilla, and that Gorilla g. graueri was intermediate in form. He attributed these anatomical differences to variation in the types of food processed, namely a large proportion of fibrous foods such as roots and bark in the diet of mountain gorillas, in contrast to the soft fruits and leaves eaten by lowland gorillas.

The incisor teeth of Gorilla are relatively small, which places them among the folivorous primates (Hylander, 1975; Shea, 1983). However molar structure is a better guide to dietary adaption than that of incisor teeth, as the back teeth have a single function - chewing (Kay & Covert, 1984), and reflect the physical nature of the foods chewed (Kay & Hylander, 1978). Gorillas' molars are adapted to shearing (e.g. Hylander, 1979; Kay, 1975). However, if the molar teeth of two subspecies of gorilla are compared, lowland gorillas fall between mountain gorillas and the frugivorous apes (Kay, 1977). Lowland gorillas have less well developed shearing crests than do the mountain subspecies, probably because they eat less fibre. Kay (pers.comm.) believes this to be a biologically significant difference, because there is very little overlap between the range of values obtained for each subspecies.

Interestingly, the molar teeth of Pan paniscus are better adapted for shearing than those of Pan troglodytes, and this is thought to reflect the high incidence of herbaceous foods eaten (Kinzey, 1984). In this respect the frugivorous bonobos resemble gorillas. Shearing is often used as an indication of folivory, but bonobos demonstrate that frugivores may also have adaptions for processing herbaceous foods.

Both gorillas and chimpanzees have thin tooth enamel compared to some other primates, such as orang-utans. This may be related to eating more soft foods, namely leaves and fruit (e.g. Kay, 1981; Martin, 1985; Teaford & Walker, 1984).

Examinations of dental microwear (i.e. microscopic scratches or striations on teeth) are also informative. Wear on the canine/premolar complex of lowland gorillas from

Cameroon indicated a diet composed primarily of leaves and pith, and fruit to a lesser extent (Ryan, 1981). However, patterns of microwear change rapidly with seasonal shifts in diet (see Kay, 1984), and would be expected to change in relation to cycles of fruit abundance. If the specimens examined by Ryan had lived in areas of predominantly secondary forest, or were killed during periods of fruit scarcity, the importance of foliage in the diet would have been over-emphasised. Ryan also found that microwear patterns on the teeth of Pan t. troglodytes resembled those of Gorilla g. gorilla, indicating that their diets were likely to have been similar.

Enamel hypoplasia (i.e. a deficiency of matrix formation or mineralization manifested as pits or grooves around the crown of a tooth) in lowland gorillas from Cameroon reflected a semi-annual cycle of systemic stresses, which would have included nutritional factors (Skinner, 1986). These stresses were thought to be related to season, and may have resulted from fruit shortages. I propose that such a cyclic pattern would have been found only among gorillas which depended on seasonally available food sources, and not among gorillas which fed primarily on ubiquitous herbaceous foods.

3. Digestive Tract

Morphological characteristics of the digestive system are closely related to diet (e.g. Hladik, 1967). For example, there is a clear differentiation between the folivorous howler monkey, Alouatta, and the frugivorous spider monkey, Ateles (Milton, 1981a).

The gorilla's gut proportions are close to those of the other (frugivorous) apes, although the small intestine is relatively smaller and the caecum is relatively larger (Milton, 1987). All the apes have large colons in relation to humans, indicating that their diets contain a considerable amount of indigestible bulk, which could be fibre or seeds (Milton, 1986).

Chivers and Hladik (1980) derived 'coefficients of gut differentiation' from the surface area of gut compartments (which reflects the area available for absorption), and found that lowland gorillas fell into the overlap between frugivores and folivores. But when coefficients were calculated from the volumes of gut compartments (which reflect the capacity for fermentation) chimpanzees tended more towards folivory than gorillas

did. However, it is difficult to draw firm conclusions from these data, as the only gorilla examined was a subadult (D. Chivers, pers.comm.), who had been released onto an island with a group of chimpanzees at M'passa in Gabon (G. Michaloud, pers.comm.).

An allometric comparison of primates' guts did "not fit with the general interpretation of the gorilla as a folivore" (Martin *et al*, 1985:76). Multivariate clustering techniques did not separate out primates with specialisations for a "fairly" large proportion of fruit in the diet, which included chimpanzees, moustached monkeys, and gorillas, from some other non-frugivorous mammals. Martin *et al* (1985) concluded that the digestive tracts of primates are unspecialised and flexible compared to those of other mammals.

Features of the gut can alter rapidly in response to a change in diet, particularly the gut proportions (see Milton, 1986). This plasticity is particularly striking when comparing captive and wild-caught primates of the same species. Some dimensions of the gastrointestinal tract of captive individuals can be modified by an artificial diet (Martin *et al*, 1985). Presumably intraspecific variation might occur in wild populations with differing diets (Sussman, 1987). If this reasoning were applied to wild gorillas, the gut could be modified according to the diet in different regions, or in different types of vegetation (i.e. mature and secondary forest). The origins of specimens so far examined may have been biased towards areas of secondary forest or plantations, to which gorillas are sometimes attracted (e.g. Blancou, 1955; Valker, 1931), or seasonal variation in fibre consumption may have affected gut dimensions. Thus inferences regarding the folivorous tendencies of gorillas may not have been drawn from a typical sample. According to Gartlan (1980) most museum specimens were obtained either in hilly country on the periphery of forested areas, or from riverine vegetation.

Perhaps we can conclude only that interpretations of anatomical data should be made with caution. However it seems likely that lowland gorillas are not as specialised for a folivorous diet as has been previously implied.

C. BODY SIZE & PHYSIOLOGY

Gorillas are the largest of all the primates, and this has important consequences for their ecology. Digestion rates are determined by gut capacity, which is ultimately constrained by body size. Milton (1980, 1981a, 1984) identified a paradox of gut retention time versus expedient digestion: fruits can be digested quickly, which allows a greater total volume of food to be processed, but complex carbohydrates, such as cellulose, and leaf proteins, take longer for extraction of nutrients to be efficient. So a compromise between efficiency and velocity must be reached when dealing with different types of food. Similar gut transit times of 36-38 hrs were recorded for three species of great apes in captivity, although gorillas retained a proportion of their food for a longer time (Milton, 1984). Digestion may have been slowed down in gorillas so that fermentation could take place, but there were no other indications that gorillas show a greater degree of adaptation to folivory in comparison to other apes (Milton, 1984).

Metabolic turn-over rates and digestive capacities are the principal size-dependent variables which set the lower limits on food choice. A large capacity and slow turn-over allow orang-utans to consume fruits with a high fibre content (Temerin *et al*, 1984). Male baboons consume a greater proportion of fibre than females, as ratios of metabolic rate:gut capacity are lowered as a result of larger body size in males, and longer gut passage times can be afforded (Demment, 1983). As gorillas are the largest apes we might expect all gorillas to eat larger amounts of fibre than other apes. Lowland gorillas probably do eat proportionately larger quantities of fibre than sympatric chimpanzees, but fibre and leaves contribute much less to the overall diet than they do to the diet of mountain gorillas. As for sex differences, neither this study nor Watts' (1984) study found any significant differences between the diets of male and female gorillas.

As body size is a major determinant of metabolic requirements, large individuals will have an increased capacity to survive periods when food intake does not meet nutritional demands, by supplementing their diets with abundant poorer quality items. Thus the constraints of limited food availability would be relaxed (Temerin *et al*, 1984). This seemed to be the strategy adopted by gorillas at Lope, who ate fibrous fruits and herbaceous foods in greater amounts when overall fruit abundance was low. These

"staple" foods were several species of Marantaceae and Aframomum, which were ubiquitous, abundant, and available during all seasons.

Basal metabolic rate is also partly determined by the costs of thermoregulation, and these costs are high when ambient temperatures drop substantially below 37°C (Dunbar, 1988:34), as they do in the cold high-altitude habitat of the Virunga Volcanoes. Therefore the metabolic needs of lowland gorillas may be lower than for mountain gorillas, as the range of ambient temperatures in tropical forest is relatively narrow.

The importance of fruit in the lowland gorilla's diet is emphasised in this thesis, but the critical role played by fibre and leaves is not denied. A ciliate, Troglodytella gorillae, which is widespread among wild gorillas in Gabon, may be evidence of the significance of fibre, if it can be demonstrated to be a symbiont involved in digestion. This large intestinal ciliate has a hydrolytic effect on cellulose *in vitro* (Collet *et al*, 1984).

D. COGNITIVE CAPACITY

To forage efficiently on fruit in an environment with dynamic and fluctuating fruit sources, consumers must be able to remember the locations and phenology patterns of fruiting trees, anticipate ripening in order to return at opportune times, recognise fruit species, and perhaps even realise that other individuals of the same species may be in fruit (e.g. Garber, 1987; Milton, 1981b). Complex feeding strategies are required which demand a complicated information processing and retrieval system (Martin, 1984). Individuals who depend on fruit sources which are unpredictable have to process a greater amount of information than others feeding on leaves, which are more evenly distributed both spatially and temporally (e.g. Walker, 1981). This is particularly so in tropical forests where the effectiveness of visual cues is reduced beyond 10-15 m.

The ability to exploit patchily distributed food sources may have been a stimulant to the development of mental capacity in primates (e.g. Milton, 1981b; Ghiglieri, 1984b). Primates have the largest ratios of brain weight to body weight among mammals (Martin, 1984), and the Pongidae have the largest comparative brain size. Diet and foraging strategy have been implicated as factors influencing brain development (Harvey *et al*, 1980), as frugivores seem to have undergone greater cerebral expansion than folivores

(Clutton-Brock & Harvey, 1980). The great apes have advanced learning skills in comparison to those of all other groups of non-human primates (e.g. Rumbaugh & Gill, 1976), and a long-term memory lasting at least 2.5 years has been demonstrated in captive gorillas (Patterson & Tzeng, 1979).

Menzel's (1973) experiments showed that chimpanzees have an acute memory of places and perception of relative distances, and that they take into account relative preferences *and* spatial clusterings *and* distance when assessing potential rewards. Mental maps would enable economy of movement between food patches, and fruit sources could be located and exploited more efficiently. Boesch and Boesch (1984) demonstrated the use of spatial memory and mental mapping on the basis of tool transportation: chimpanzees were able to remember locations and compare them, combining information about weight and distance. The Boesches speculated that the exploitation of a rich and patchy food source (nuts) in an environment with poor visibility (<20 m) contributed to the development of spatial capacity in the Tai chimpanzee population. Similarly the highly developed spatial skills of nomadic hunter-gatherers compared to those of sedentary agrarian peoples may be attributable to ecological demands (Dasen, 1975).

At Lope excursions to food sources with limited temporal availability, such as Uapaca trees in gallery forests, suggested that gorillas were capable of mental mapping, and of judging the timing of fruit production, as they visited the galleries only at particular times of the year. If lowland gorillas require greater intelligence to exploit food sources in tropical forests than do mountain gorillas living in a less heterogeneous and less complex environment, one might expect to find evidence to support this. An indication that subspecific differences in brain function exist comes from the asymmetry of the gorilla's cerebral hemispheres, as described by Groves and Humphrey (1973).

E. DIET & EVOLUTION

A combination of flexible mental strategies and physiological morphology are required to adjust to and exploit a range of environmental conditions (e.g. Hladik, 1981).

The adaptability of gorillas at Lope has been demonstrated by their use of both extremes of their habitat: the dense, wet Marantochloa marshes and streams, and the dry, open savannas. Differences in the diets of Gorilla g. beringei and Gorilla g. graueri are adaptions to local changes in floristic composition (Goodall, 1977), and mountain gorillas in Zaire have adapted to pressure for intensive land use by foraging in fallow fields, sometimes only 30 m from houses (Aveling & Aveling, 1987). The range of gorillas' adaptation is indicated by their broad diets and their wide distribution, from lowland tropical forest to high altitude montane regions.

Groves (1971) proposed that gorillas evolved in the montane regions of East Africa, radiating into the lowland forests of West Africa. However, there is substantial evidence that primates originated in tropical forest environments (e.g. Andrews & Aiello, 1984; Susman, 1987), and that fruit was the main constituent of the hominoid ancestor's diet during the Miocene (Boyd Eaton & Konner, 1985). It is improbable that gorillas evolved from a frugivorous ancestor to become folivores, only to move back into a frugivous niche. It seems much more likely that mountain gorillas are secondarily adapted to their specialised diet. It is possible that the gorillas of Gabon show least adaptation towards exploiting regenerating vegetation and cultigens than gorillas in more densely populated regions of West Africa, where land-use is intensive and cultivation widespread, as cultivation did not become important in Gabon until the 1920s (Gautier-Hion, 1971). However, the gorilla's tendency to switch to a higher fibre diet when fruit is less abundant may have facilitated a move into a more folivorous niche in other parts of their geographic range. Frugivory in extant hominoids justifies the assumption that this was the ancestral dietary type for the Hominoidea (Andrews & Aiello, 1984), and this argument is more convincing if all four species of great ape are now seen to be primarily frugivorous.

F. DIET & SOCIALITY

Feeding has been termed a 'primary ecological determinant' and treated as a key variable in functional models of co-evolved behavioural and ecological traits (see Kurland & Gaulin, 1987). Dietary regimes impose constraints on body size, locomotion,

breeding strategy, and social behaviour, and these factors limit geographic range and habitat (e.g. Walker, 1981). Thus frugivory is likely to have a strong impact on other aspects of the lowland gorilla's ecology, and this will contribute to our understanding of socioecology.

Group living by gorillas has been explained by hypothesised increases in foraging efficiency and the exchange of information about food sources (cohesion within a social unit would allow transmission of important information regarding the location and phenology of fruit sources). Such explanations concerned the benefits of social learning, and the development of stable social relationships (e.g. Fossey & Harcourt, 1977; Milton & May, 1976).

More recently these ideas have been refined. Wrangham (1979, 1986) named food as the primary selection pressure on female grouping (for males it is females), and proposed that the grouping patterns of great apes are constrained by feeding competition. Sugardjito *et al* (1987) found that the time spent socialising by orang-utans increased with fruit availability (cf. Ghiglieri, 1984a; Wrangham, 1977). Temporary surfeits of fruit minimised competition between individuals, so that orang-utans were able to form temporary parties.

Differences in the social structure of two populations of bonobos reflect different ecological pressures (Susman, 1987), and party size at Lomako is positively correlated with the phenology of favoured fruits (Badrian & Malenky, 1984). Foraging may also be primarily responsible for differences in aspects of the social organisation of chimpanzees and bonobos (Wrangham, 1986). Wrangham proposed that competition between bonobos may be less severe as a result of access to THV (terrestrial herbaceous vegetation), which occurs widely throughout their geographic range and is eaten extensively (Badrian & Badrian, 1984; Badrian & Malenky, 1984; Kano & Mulavwa, 1984). THV is used more by bonobos than chimpanzees, and Wrangham (1986) proposed that a lack of THV in the chimpanzee's diet is due to competition with sympatric gorillas. However, competition for this resource is likely to be very low at Lope, as THV is abundant (Rogers & Williamson, 1987), and the same may be true of other areas where gorillas and chimpanzees are sympatric. The proportions of Marantaceae foods in the diets of the chimpanzees and

gorillas at Lope could be equivalent. The only obvious difference seen was that gorillas consumed more Aframomum pith, which is very fibrous and requires a lot of chewing. As chimpanzees are not well adapted to shearing (Kinzey, 1984), morphological differences might account for the divergence in the apes' diets. Body size will also be a relevant factor, determining nutritional requirements, and enabling gorillas to eat larger quantities of low quality foods such as Aframomum.

Ghiglieri (1987) contrasted the fission-fusion society of chimpanzees with that of the more solitary orang-utans, explaining their differences on the basis of food distribution, foraging strategies, and locomotion costs. Lowland gorillas seem to have an intermediate social structure, and it has been assumed that their stable group formation is possible because they have a diet consisting solely of abundant herbs. Wrangham (1986) stated that THV is the principal food of gorillas and that fibrous foods may allow gorillas to live in groups.

If limits to group size are set by the importance of feeding competition, groups should be smaller where feeding competition is higher. The reliable production and plentiful distribution of mountain gorillas' foods enable members of a group to forage together and to remain together on a permanent basis. Feeding competition between mountain gorillas is correlated with group size, but individuals make little nutritional sacrifice, as the effects of competition are ameliorated by the relatively even dispersion of food (Watts, 1985). The gorillas at Lope eat large amounts of fruit, for which there may be considerable intra- and inter-specific competition. Dunbar (1988:314) noted that in poorer quality habitats excessive travel costs could be avoided by a decline in party size. Presumably, this would also apply to habitats with widely dispersed resources, or where there is a seasonal reduction in the quality of foods available. But despite these two constraints gorilla groups at Lope do not seem to be smaller than mountain gorilla groups. Given the fluid social structure of chimpanzees and bonobos, we might also expect lowland gorillas to have a more flexible system than that of mountain gorillas. Maryanski (1987) contended that the social structure of gorillas should not be seen as consisting of discrete groups, but viewed at a community level. Maryanski proposed that there are weak social ties between all individuals in a community, and as evidence for this cites the

overlapping use of home ranges and transfer of individuals between groups. I believe that tolerance is a more appropriate concept here than social ties. Gorillas do not have exclusive home ranges, but there is no evidence of community boundaries, as there is for chimpanzees (Goodall *et al*, 1979; Nishida, 1979). It is not yet apparent whether lowland gorillas are more flexible in their social relations than mountain gorillas, although at Lope the groups observed were relatively stable, in that they stayed together for several months, at least.

To resist ecological pressure towards group fission, lowland gorillas must have some other way of coping with succulent fruit shortages. The role of THV, as a reducer of competition, may help to explain why lowland gorillas are able to remain together. Perhaps the switch in diet, facilitated by large body size, produces a greater resistance to succulent fruit shortages, and allows the gorillas to live in stable groups. The fibrous fruits eaten at Lope would be important in this context.

Ecological factors influence and may limit the expression of sociality in great apes, but social priorities may supersede predictions concerning competition (Ghiglieri, 1987). Vulnerability to conspecifics may be the principal source of social bonds, and defensive groups will form when foraging constraints permit (Wrangham, 1986). Whatever factors determine the social structure of gorillas, the relative uniformity of group size across populations implies that similar processes are maintaining this structure (Harcourt *et al*, 1981).

Wrangham (1986) described bonobos as combining elements of chimpanzee and gorilla feeding ecology, with the THV of gorillas and fruits of chimpanzees. However, the lowland gorilla is an intermediate between chimpanzees and mountain gorillas, so perhaps a new locus should be defined on this ecological dimension, which could account for the gradation of strategies from chimpanzee to bonobo to lowland gorilla to mountain gorilla.

G. CONCLUSIONS

There is a pervasive view in the published literature that chimpanzees in fission-fusion societies feeding on fruit in 'primary forest' exist at one end of a multi-dimensional ecological spectrum, and that gorillas living in stable groups and

feeding on foliage in secondary vegetation are at the other (e.g. Dixson, 1981; Dunbar, 1988; Ghiglieri, 1987; Jones & Sabater Pi, 1971; Maryanski, 1987; Wrangham, 1986). The present study shows that the frugivorous feeding strategy of lowland gorillas largely resembles that of chimpanzees and bonobos, although lowland gorillas focus on poorer quality fibrous foods to relieve food competition, and to reduce travel costs when succulent fruits are in short supply. This shift in the diet may help gorillas to remain in stable groups during periods of nutritional stress.

The differences between the feeding, ranging, and climbing behaviour of lowland and mountain gorillas result from striking differences in their respective habitats, especially in the abundance and distribution of fruit sources. Whether or not these differences have produced divergent social structures remains to be seen, but at a superficial level the gorillas at Lope have the same group structure as seen in other populations. Further study of these apes may reveal subtle and interesting differences in their social behaviour.

As there is no neat folivore/frugivore division between lowland gorillas and chimpanzees, the niche to which lowland gorillas have been assigned should now be evaluated.

Appendix 1.1 Some Mammal and Bird Species Identified at Lope

MAMMALS

Bdeogale nigripes	black-footed mongoose
Cephalophus dorsalis	bay duiker
Cephalophus leucogaster	white-bellied duiker
Cephalophus monticola	blue duiker
Cephalophus sylvicultor	yellow-backed duiker
Dendrohyrax arboreus	tree dassie
Genetta sp.	genet
Herpestus paludinosus	marsh mongoose
Hymoschus aquaticus	water chevrotain
Loxodonta africana cyclotis	forest elephant
Manis tricuspis	three-cusped pangolin
Mellivora capensis	ratel
Nandinia binotata	two-spotted palm civet
Panthera pardus	leopard
Potamochoerus porcus	bush pig
Profelis aurata	golden cat
Syncerus caffer nanus	buffalo
Thryonomys swinderianus	cane rat
Tragelaphus scriptus	bush buck
Tragelaphus spekii	sitatunga
Viverra civetta	African civet

Primates

Arctocebus calabarensis	golden potto
Cercocebus albigena	grey-cheeked mangabey
Cercopithecus cephus	moustached monkey
Cercopithecus nictitans	greater white-nosed monkey
Cercopithecus pogonias	crowned guenon
Colobus satanas	black colobus
Galago demidovii	dwarf galago
Gorilla gorilla gorilla	gorilla
Pan troglodytes troglodytes	chimpanzee
Mandrillus sphinx	mandrill
Perodicticus potto	potto

BIRDS

black and white tailed hornbill
black casqued hornbill
brown cheeked hornbill
red billed dwarf hornbill
white crested hornbill
brown necked parrot
grey parrot
bareheaded rock fowl
blue breasted kingfisher
blue plantain eater
crested guinea fowl
crowned hawk eagle
palm nut vulture
pygmy kingfisher
shining blue kingfisher
scaly francolin
Senegal thick knee
Verreaux's touraco
Vinaceous dove

Appendix 3.1 Phytosociological Table of Tree Species Produced by TWINSPAN

MEAN BASAL AREA (m2/ha) PER SPECIES IN EACH VEGETATION CLASS

Species	A	B	C	D	E	F	G	H	I	J
44	0.00	0.00	0.34	0.01	0.00	0.00	0.00	0.00	0.00	0.00
34	0.00	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.00	0.00
51	0.00	0.00	0.00	1.43	0.00	0.00	0.00	0.00	0.00	0.00
54	0.00	0.00	0.00	3.44	0.00	0.00	0.00	0.00	0.00	0.00
61	0.00	0.19	0.45	1.02	0.03	0.03	0.00	0.00	0.00	0.00
11	0.06	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00
62	0.12	0.48	0.00	0.00	3.33	0.00	0.00	0.00	0.00	0.00
46	0.32	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.10	0.00
41	3.93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
49	0.86	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00
35	0.36	0.00	0.00	0.08	0.65	0.00	0.00	0.00	0.00	0.00
32	4.23	1.82	0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.00
42	1.02	0.00	0.00	0.58	0.00	0.00	0.00	0.00	0.00	0.00
13	1.87	0.00	2.37	0.00	1.37	0.00	0.00	0.00	0.00	0.00
38	1.34	0.92	0.15	1.07	0.85	0.00	0.04	0.00	0.00	0.09
58	0.07	0.00	0.07	0.14	0.00	0.00	0.00	0.00	0.00	0.00
23	0.93	10.89	5.87	0.00	0.00	0.00	0.45	0.00	0.00	0.00
33	0.40	7.05	1.62	1.16	0.95	0.00	0.15	0.00	1.23	0.00
7	1.35	7.62	9.50	8.99	6.35	2.09	1.90	0.43	0.63	0.92
22	0.85	0.06	0.87	0.80	1.00	0.00	0.26	0.05	0.08	0.00
45	0.64	0.00	0.00	3.80	27.42	0.09	0.00	0.00	0.68	0.00
50	0.00	0.00	0.00	0.79	0.19	0.00	0.00	0.00	0.45	0.00
9	0.22	1.65	0.50	4.01	2.34	0.17	0.45	0.78	1.65	0.00
52	0.00	0.00	0.00	1.36	1.04	0.00	0.00	0.50	1.05	0.00
12	0.00	0.00	4.41	0.17	0.00	0.00	0.00	0.00	2.41	0.00
40	0.00	0.00	0.14	0.38	0.00	0.00	0.15	0.13	0.20	0.08
59	0.00	0.00	0.00	0.40	0.10	0.95	0.00	0.00	0.00	0.00
63	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.49	0.00
31	0.30	0.46	0.27	0.67	0.20	0.55	0.20	0.13	0.29	0.00
48	0.51	0.00	0.00	0.58	0.00	0.48	0.00	0.00	0.02	0.00
17	0.16	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.09	0.00
47	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
4	1.06	0.00	0.00	0.21	0.00	2.55	0.00	0.00	0.00	0.00
18	0.68	3.47	0.00	0.85	0.00	0.18	0.97	1.60	0.03	0.00
30	0.66	0.00	0.00	0.44	0.00	1.45	0.15	0.00	0.00	0.00
36	0.64	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00
14	0.14	0.00	0.00	0.91	0.00	0.00	0.23	0.45	1.02	0.00
16	0.74	0.00	0.00	1.19	0.00	0.41	1.05	0.00	0.62	0.00
15	2.76	0.00	0.00	0.00	0.00	0.32	0.69	1.76	0.00	0.00
19	2.72	0.00	0.00	0.00	0.36	0.31	0.73	3.46	0.00	0.00
20	0.14	0.00	0.00	0.00	0.00	0.00	0.02	0.38	0.00	0.00
8	0.00	2.19	0.00	0.00	0.00	0.95	0.00	0.00	0.00	1.65
26	1.55	0.00	2.68	1.15	1.48	5.09	1.41	0.00	1.02	5.44
60	0.00	0.00	0.00	0.10	0.00	0.06	0.00	0.00	0.04	0.00
1	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.00	2.13	0.00
2	0.00	0.00	4.67	0.00	0.00	0.00	0.96	0.00	4.58	0.00
3	0.00	0.00	0.06	0.09	0.00	0.00	0.17	0.00	0.48	0.00
57	0.00	0.00	0.00	0.15	0.00	0.00	0.33	0.00	0.53	0.00
27	0.02	0.00	0.00	0.01	0.00	0.00	0.06	0.06	0.44	0.42
55	0.00	0.00	0.00	0.02	0.00	0.25	0.03	0.00	0.89	0.53
39	0.00	0.04	0.00	0.00	0.00	0.23	0.14	0.00	0.78	0.85
56	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.08	0.00
6	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.53
53	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	2.42
66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.70	0.00
10	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.09	0.14	0.00
67	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.63	0.00
21	1.37	0.00	0.00	0.08	0.27	0.29	2.19	0.81	3.34	0.13
24	0.04	0.00	0.00	0.01	0.00	0.37	0.12	0.13	0.02	0.00
28	0.00	0.00	0.15	0.03	0.22	0.17	0.22	0.08	0.25	0.00
64	0.00	0.05	0.00	0.00	0.00	0.06	0.02	0.00	0.00	0.18
5	0.04	0.00	0.00	0.00	0.00	0.17	0.08	0.00	0.06	0.00
25	0.00	0.00	0.00	0.00	0.00	0.00	0.19	8.92	0.00	0.00
29	0.00	0.00	0.00	1.61	5.21	11.08	22.85	4.52	4.12	0.00
37	0.00	0.00	0.00	0.00	0.00	3.25	0.00	0.00	0.00	0.00
65	0.00	0.00	0.00	0.00	0.00	0.00	2.10	0.00	0.00	0.00
43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TOTALS	32.33	36.87	34.63	40.03	53.74	31.53	38.57	24.31	31.53	13.25

Appendix 3.1. Tree Species Identified on Transects at Lope

SEGC No.	SPECIES	FAMILY	No. of trees
65	Anthonotha macrophylla	CAESALPINIACEAE	27
78	Aucoumea klaineana	BURSERACEAE	45
72	Barteria fistulosa	PASSIFLORACEAE	18
141	Beilschmiedia sp	LAURACEAE	1
64	Berlinea bracteosa	CAESALPINIACEAE	32
73	Brachystegia aff. eurycoma	CAESALPINIACEAE	6
1	Canarium schweinfurthii	BURSERACEAE	2
113	Carapa procera	MELIACEAE	1
171	Cassia sp	CAESALPINIACEAE	10
100	Ceiba pentandra	BOMBACACEAE	1
17	Celtis tessmannii	ULMACEAE	3
187	Chlorophora excelsa	MORACEAE	4
33	Cola lizae	STERCULIACEAE	394
61	Cryptosepalum staudtii	CAESALPINIACEAE	45
51	Dacryodes buettneri	BURSERACEAE	11
28	Dacryodes normandii	BURSERACEAE	5
197	Desbordesia sp	IRVINGIACEAE	3
82	Detarium macrocarpum	CAESALPINIACEAE	2
79	Dialium sp	CAESALPINIACEAE	18
45	Diospyros cf iturensis	EBENACEAE	1
169	Diospyros cf viridicans	EBENACEAE	4
70	Diospyros dendo	EBENACEAE	105
43	Diospyros polystemon	EBENACEAE	84
44	Diospyros suaveolens	EBENACEAE	4
63	Discoglypremna coloneura	EUPHORBIACEAE	4
62	Distemonanthus bethamianus	CAESALPINIACEAE	11
59	Duboscia macrocarpa	TILIACEAE	9
49	Elaesis guineensis	PALMAE	2
98	Enantia chlorantha	ANNONACEAE	4
137	Eriocoelum macrocarpum	SAPINDACEAE	1
138	Eriocoelum ?panisculatum	SAPINDACEAE	4
260	Eriocoelum sp	SAPINDACEAE	1
261	Eriocoelum sp	SAPINDACEAE	1
102	Erythroxylum mannii	ERYTHROXYLACEAE	4
183	Euonymus congolensis	CELASTACEAE	22
106	Fagara ?macrophylla	RUTACEAE	2
97	Ficus thonningii	MORACEAE	3
135	Garcinia cf kola	GUTTIFERAE	1
210	Gilbertiodendron dewevrei	CAESALPINIACEAE	4
238	Guibortia demeusii	CAESALPINIACEAE	1
204	Harungana sp	HYPERICACEAE	4
8	Heisteria parvifolia	OLACACEAE	10
48	Hexalobus crispiflora	ANNONACEAE	6
83	Hylodendron gabunense	CAESALPINIACEAE	15
114	Hypodaphnis zenkeri	LAURACEAE	5
107	Irvingia gabonensis	IRVINGIACEAE	5
71	Irvingia grandiflora	IRVINGIACEAE	7
88	Klainedoxa gabonensis	IRVINGIACEAE	3
209	Klainedoxa sp.	IRVINGIACEAE	1
67	Lophira alata	OCHNACEAE	61
205	Lovoa trichilioides	MELIACEAE	1

Appendix 3.1. Tree Species Identified on Transects at Lope (cont.)

SEGC No.	SPECIES	FAMILY	No. of trees
30	Maranthes gabunensis	CHRYSOBALANACEAE	2
212	Maranthes glabra	CHRYSOBALANACEAE	1
101	Milletia versicolor	PAPILIONACEAE	7
198	Milletia sp	PAPILIONACEAE	1
95	Myrianthus arboreus	MORACEAE	7
66	Nauclea didderichi	RUBIACEAE	3
263	Nauclea vanderguchtii	RUBIACEAE	1
116	Neochevalierodendron stephanii	CAESALPINIACEAE	8
201	Ochna sp	OCHNACEAE	1
60	Ongokea gore	OLACACEAE	7
81	Panda oleosa	PANDACEAE	1
93	Pausinystalia macroceras	RUBIACEAE	25
85	Pentaclethra eetveldeana	MIMOSACEAE	26
74	Pentaclethra macrophylla	MIMOSACEAE	28
140	Pentadesma butyracea	GUTTIFERAE	1
92	Phyllanthus discoideus	EUPHORBIACEAE	28
84	Piptadeniastrum africanum	MIMOSACEAE	2
90	Plagiostyles africana	EUPHORBIACEAE	5
9	Polyalthia suaveolens	ANNONACEAE	13
159	Porterandia cladantha	RUBIACEAE	5
142	Pseudospondias longifolia	ANACARDIACEAE	1
96	Pseudospondias microcarpa	ANACARDIACEAE	5
99	Pterocarpus soyauxii	PAPILIONACEAE	14
3	Pycnanthus angolensis	MYRISTICACEAE	3
175	Saccoglottis gabonensis	HUMIRIACEAE	1
23	Santiria trimera Types I and II	BURSERACEAE	4
86	Sterculia tragacantha	STERCULIACEAE	3
222	Strombosiopsis cf tetrandra	OLACACEAE	3
109	Swartzia fistuloides	CAESALPINIACEAE	8
108	Testulea gabonensis	LUXEMBURGIACEAE	5
94	Tetrapleura tetraptera	MIMOSACEAE	2
133	Treculia africana	MORACEAE	1
91	Trichilia prieureana vermoesnii	MELIACEAE	79
76	Trichoscypha acuminata	ANACARDIACEAE	15
10	Uapaca guineensis	EUPHORBIACEAE	1
231	Vitex sp	VERBENACEAE	2
232	Vitex sp	VERBENACEAE	1
87	Xylopia aethiopica	ANNONACEAE	35
75	Xylopia hypolampra	ANNONACEAE	15
80	Xylopia ?quintasii	ANNONACEAE	57
34	Zanha golungensis	SAPINDACEAE	4
235	Crudia sp.	CAESALPINIACEAE	1
185		EUPHORBIACEAE	19
243		RUBIACEAE	1
229		RUBIACEAE	1
105		RUTACEAE	7

substituted for Appendix 4.1 - table from AJP paper

Species of plants and their parts eaten by gorillas at Lope, Gabon 1984-1989

Scientific Name	Family	Pulp	Seed	Leaf	Stem	Bark	Other
Aframomum longipetiolatum	ZINGIBERACEAE	x			x		
Aframomum sp. nov.	ZINGIBERACEAE	x			x		
Aframomum ?leptolepis	ZINGIBERACEAE	x			x		
Anchomanes difformis	ARACEAE			x	x		
Anisotes macrophyllus	ACANTHACEAE			x			
Antidesma vogelianum	EUPHORBIACEAE	x					
Antidesma sp #251	EUPHORBIACEAE	x					
Anthocleista ?vogelii	LOGANIACEAE			x			
Antrocaryon klaineanum	ANNONACEAE	x					
Ataenidia conferta	MARANTACEAE			x			
Aucoumea klaineana	BURSERACEAE						flowers
Berlinea bracteosa	CAESALPINIACEAE			x			
Brachystegia aff. eurycoma	CAESALPINIACEAE		x				
Celtis tessmannii	ULMACEAE	x		x			
Chlorophora excelsa	MORACEAE			x		x	
Chrysophyllum subnudum	SAPOTACEAE	x					
Cissus leonardi	VITACEAE	x					
Cissus sp #145	VITACEAE	x		x			
Cola lizae	STERCULIACEAE	x		x			
Costus afer	ZINGIBERACEAE			x			
Cryptosepalum staudtii	CAESALPINIACEAE		x	x			
Dacryodes normandii	BURSERACEAE	x					
Detarium macrocarpum	CAESALPINIACEAE		x	x			
Dialium sp #79	CAESALPINIACEAE	x	x	x			
Dialium sp #118	CAESALPINIACEAE	x					
Dichapetalum ?unguiculatum	DICHAPETALACEAE		x				
Diospyros abyssinica	EBENACEAE	x					
Diospyros cf. iturensis	EBENACEAE	x	x				
Diospyros cf. viridicans	EBENACEAE			x			
Diospyros dendo	EBENACEAE	x	x				
Diospyros polystemon	EBENACEAE	x	x				
Diospyros suaveolens	EBENACEAE	x	x				
Drypetes sp# 264	EUPHORBIACEAE	x					
Duboscia macrocarpa	TILIACEAE	x					
Enantia chlorantha	ANNONACEAE	x					
Eremospatha cabrae	PALMAE	x		x	x		
Ficus macrosperma	MORACEAE	x					
Ficus mucuso	MORACEAE	x		x			
Ficus ?polita	MORACEAE	x					
Ficus recurvata	MORACEAE	x					
Ficus thonningii	MORACEAE	x					
Gambeya africana	SAPOTACEAE	x					
Grewia sp # 343	ANACARDIACEAE	x					
Halopegia azurea	MARANTACEAE			x	x		
Haumania liebrechtsiana	MARANTACEAE		x	xx			
Heisteria parvifolia	OLACACEAE	x		x			
Heisteria sp #110	OLACACEAE			x			
Hexalobus crispiflorus	ANNONACEAE	x					
Hypselodelphis violacea	MARANTACEAE		x	xx			
Irvingia gabonensis	IRVINGIACEAE	x					
Irvingia grandiflora	IRVINGIACEAE	x					
Klainedoxa gabonensis	IRVINGIACEAE	x					
Klainedoxa sp #208	IRVINGIACEAE	x					
Leptoderris sp #57	PAPILIONACEAE			x			
Lecaniodiscus cupanoides	SAPINDACEAE	x					
Lophira alata	OCHNACEAE			x			

Species of plants and their parts eaten by gorillas at Lope, Gabon (cont.)

Scientific Name	Family	Pulp	Seed	Leaf	Stem	Bark	Other
Mammea africana	GUTTIFERAE	x					
Mangifera indica	ANNONACEAE	x					
Marantochloa cordifolia	MARANTACEAE			x	x		
Marantochloa filipes	MARANTACEAE				x		
Marantochloa purpurea	MARANTACEAE			x	x		
Megaphrynium gabonense	MARANTACEAE	x		xx	x		roots
Megaphrynium macrostachyum	MARANTACEAE	x		xx	x		
Milletia versicolor	PAPILIONACEAE			x		x	
Monanthotaxis congensis	ANNONACEAE	x					
Monodora angolensis	ANNONACEAE	x					
Myrianthus arboreus	MORACEAE	x				x	
Nauclea didderichi	RUBIACEAE	x					
Nauclea vandeguchtii	RUBIACEAE	x					
Oncoba spinosa	FLACOURTIACEAE			x			
Palisota ambigua	COMMELINACEAE				x		
Parkia bicolor	MIMOSACEAE	x					
Parkia filicoidea	MIMOSACEAE	x					
Pausinystalia macroceras	RUBIACEAE			x			
Pavetta puberula	RUBIACEAE			x			
Pentaclethra eetveldeana	MIMOSACEAE			x			
Pentaclethra macrophylla	MIMOSACEAE			x			
Pentadesma butyracea	GUTTIFERAE	x	x				
Piptadeniastrum africanum	MIMOSACEAE		x				
Plagiostyles africana	EUPHORBIACEAE	x					
Porterandia cladantha	RUBIACEAE	x					
Pseudospondias longifolia	ANACARDIACEAE	x					
Pseudospondias microcarpa	ANACARDIACEAE	x					
Psidium sp #53	MYRTACEAE	x					
Psychotria peduncularis	RUBIACEAE	x					
Psychotria vogeliana	RUBIACEAE	x					
Pterocarpus soyauxii	PAPILIONACEAE		x	x			flowers
Renealmia cincinnata	ZINGIBERACEAE				x		
Renealmia macrolea	ZINGIBERACEAE				x		
Rutidea dupuisii	RUBIACEAE	x					
Saccoglottis gabonensis	HUMIRIACEAE	x					
Santiria trimera Types I-II	BURSERACEAE	x					
Scyphocephalium ochocoa	MYRISTICACEAE			x			
Scytopetalum ?klaineanum	SCYTOPETALACEAE	x					
Swartzia fistuloides	CAESALPINIACEAE			x			
Testulea gabonensis	LUXEMBURGIACEAE			x			
Trachyphrynium braunianum	MARANTACEAE				x		
Treculia africana	MORACEAE	x					
Trichoscypha acuminata	ANACARDIACEAE	x					
Uapaca ?acuminata	EUPHORBIACEAE	x					
Uapaca guineensis	EUPHORBIACEAE	x					
Uapaca cf. sansibarica	EUPHORBIACEAE	x					
Uapaca sp #299	EUPHORBIACEAE	x					
Uvaria sp # 256	ANNONACEAE	x					
Vitex doniana	VERBENACEAE	x					
Xylopia aethiopica	ANNONACEAE	x					
Xylopia hypolampra	ANNONACEAE	x					
Xylopia ?quintasii	ANNONACEAE	x					
Zanha golungensis	SAPINDACEAE	x					
SEGC #36	APOCYNACEAE	x					
SEGC #46	APOCYNACEAE	x					
SEGC # 58	APOCYNACEAE	x					

Species of plants and their parts eaten by gorillas at Lope, Gabon (cont.)

Scientific Name	Family	Pulp	Seed	Leaf	Stem	Bark	Other
SEGC # 56	CELASTRACEAE	x					
SEGC # 319	MELASTOMATACEAE			x			
SEGC # 351	PALMAE				x		
SEGC # 288	RUBIACEAE	x					
SEGC # 291	RUBIACEAE	x					
SEGC # 369	RUBIACEAE			x			
SEGC # 318	SAPOTACEAE	x					
subtotals		79	14	43	16	3	3
unidentified foods		6	2	7		5	4
TOTALS		85	16	50	16	8	7

Appendix 4.2 F1 and F2 Values Calculated For Each Fruit Species Recorded in Gorillas' Dung

SEGC No.*	F1	F2	No. OF OCCURENCES IN DUNG
8	.4700	.1700	39
9	.7200	.3700	4
10	1.4100	1.1100	122
14	4.9300	1.9500	2
16	4.4435	2.9945	241
17	2.4100	1.1800	35
23	4.2200	1.6400	34
30	11.3800	6.4800	7
33	5.6000	1.4000	66
34	1.9500	1.1100	51
36	5.4300	1.4100	10
39	.9287	.5851	46
40	8.3800	1.5900	1
43	.7300	.4600	53
44	2.4100	1.5100	6
45	1.4100	.8400	2
48	1.3200	.7500	18
49	.4700	.1700	1
52	28.2500	22.1700	2
53	5.9350	1.9353	96
54	.9100	.2100	8
56	6.6000	4.9300	4
59	25.0001	2.5000	229
66	12.6061	11.0798	34
69	.7100	.1900	8
70	.1800	.0800	32
71	113.0000	97.3000	1
75	.4700	.1700	45
79	.6000	.1500	130
80	.4700	.1700	1
84	.2600	.2600	1
88	35.1371	8.7843	89
89	.1700	.0900	1
95	1.2000	.6600	7
96	3.3500	2.5100	20
97	4.7950	4.3840	10
98	3.0800	1.5600	2
111	.5100	.2500	48
112	1.2268	.5642	49
125	.7300	.2600	31
126	1.2330	.5670	2
139	1.3200	1.2000	1
140	25.7113	16.3617	92
141	8.7700	3.3500	1
145	2.9500	2.3900	22
159	19.6850	16.9710	47
161	5.5800	.7600	1
162	.9700	.3400	1
168	2.2600	1.4200	42
170	.1200	.0200	2
172	2.9793	1.9686	35
181	11.3904	7.5264	1
182	.4700	.1700	1
199	.4700	.1700	1

* see Appendix 4.1 for SEGC species codes

REFERENCES

Aldrich-Blake, F.P.G. (1978) Dispersion and food availability in Malaysian forest primates. In: Chivers, D.J. & Herbert, J. (eds.) Recent Advances in Primatology Volume 1, Academic Press, London, pp.323-325.

Alexandre, D.Y. (1978) Le role disseminateur des elephants en foret de Tai, Cote-d'Ivoire. La Terre et la Vie 32: 47-72.

Alexandre, D.Y. (1980) Charactere saisonnier de la fructification dans une forest hygrophile de Cote-D'Ivoire. Revue d'Ecologie (Terre et Vie) 34: 335-350.

Alexandre, D.Y. (1984) Strata in tropical rain forest at Tai (Ivory Coast). In: Chadwick, A.C. & Sutton, S.L. (eds.) Tropical Rain-Forest: The Leeds Symposium, Blackwell, Oxford, pp.15-24.

Allen, J.G. (1931) Gorilla hunting in southern Nigeria. Nigerian Field 1: 4-9.

Anderson, J.R. (1984) Ethology and ecology of sleep in monkeys and apes. Advances in the Study of Behaviour 14: 165-229.

Anderson, J.R., Williamson, E.A. & Carter, J. (1983) Chimpanzees of Sapo Forest, Liberia: density, nests, tools and meat-eating. Primates 24: 594-601.

Andrews, P. & Aiello, L. (1984) An evolutionary model for feeding and positional behaviour. In: Chivers, D.J., Wood, B.A. & Bilsborough, A. (eds.) Food Acquisition & Processing in Primates, Plenum Press, London, pp.429-466.

Anon (1934) Notes on the gorilla. Nigerian Field 3: 92-102.

Aschemeier, C.R. (1921) On the gorilla and the chimpanzee. Journal of Mammalogy 2: 90-91.

Aschemeier, C.R. (1922) Beds of the gorilla and chimpanzee. Journal of Mammalogy 3: 176-178.

Aubreville, A. (1967) La foret primaire des montages de Belinga. Biologia Gabonica 3: 95-112.

Aubreville, A. (1968) Les Cesalpinioidees de la flore Camerouno-Congolaise. Considerations taxonomiques, chorologiques, ecologiques, historique et evolutives. Adansonia 8: 147-175.

Augspurger, C.K. (1982) A cue for synchronous flowering. In: Leigh, E.G., Rand, A.S. & Windsor, D.M. (eds.) The Ecology of a Tropical Forest: Seasonal Rhythms & Long Term Changes, Smithsonian Institution Press, Washington D.C., pp.130-150.

Aveling, R. & Aveling, C. (1987) Report from the Zaire gorilla conservation project. Primate Conservation 8: 162-164.

Badrian, A. & Badrian, N. (1984) Social organisation of Pan paniscus in the Lomako Forest, Zaire. In: Susman, R.L (ed.) The Pygmy Chimpanzee. Evolutionary Biology & Behavior, Plenum Press, London, pp.325-346.

Badrian, N. & Malenky, R.K. (1984) Feeding ecology of Pan paniscus in the Lomako forest, Zaire. In: Susman, R.L (ed.) The Pygmy Chimpanzee. Evolutionary Biology & Behavior, Plenum Press, London, pp.275-299.

Baldwin, L.A. & Teleki, G. (1973) Field research on chimpanzees and gorillas: an historical, geographical and bibliographic listing. Primates 14: 315-330.

Baldwin, P.J. (1979) The natural history of the chimpanzee (Pan troglodytes verus) at Mt. Assirik, Senegal. PhD Thesis, University of Stirling.

Baldwin, P.J., Sabater Pi, J., McGrew, W.C. & Tutin, C.E.G. (1981) Comparisons of nests made by different populations of chimpanzees (Pan troglodytes). Primates 22: 474-486.

Baranga, D. (1986) Phenological observation on two food-tree species of colobus monkey. African Journal of Ecology 24: 209-214.

Barret, J. (1983) Population. In: Barret, J. (ed.) Geographie et Cartographie du Gabon, EDICEF, Paris, pp.48-51.

Bates, G.L. (1905) Notes on the mammals of Southern Cameroons and the Benito. Proceedings of the Zoological Society of London 75: 65-85.

Baulieu, E.E. (1980) The Centre International de Recherche Medicale de Franceville (CIRMF) and the symposium on the great apes of Africa. In: Short, R.V. & Wier, B.J. (eds.) The Great Apes of Africa, Journal of Reproduction & Fertility Supplement No. 28, Cambridge, pp.1-2.

Baumgartel, M.W. (1958) The Muhavra gorillas. Primates 1: 79-83.

Bawa, K.S. & Opler, P.A. (1974) Dioecism in tropical forest trees. Evolution 29: 167-179.

Bazzaz, F.A. & Picket, S.T.A. (1980) Physiological ecology of tropical succession: a comparative review. Annual Review of Ecology & Systematics 11: 287-310.

Bernstein, I.S. (1962) Response to nesting materials of wild born and captive born chimpanzees. Animal Behaviour 10: 1-6.

Bernstein, I.S. (1969) A comparison of the nesting patterns among the three great apes. In: Bourne, G.H. (ed.) The Chimpanzee, Karger, Basel, pp.393-402.

Bingham, H.C. (1932) Gorillas in a Native Habitat. Carnegie Institution of Washington, Washington D.C.

Blancou, L. (1951) Notes sur les mammiferes de l'equateur Africain Francais. 1. Gorille. Mammalia 15: 143-151.

Blancou, L. (1955) The lowland gorilla. Animal Kingdom 58: 162-169.

Boesch, C. & Boesch, H. (1984) Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. Primates 25: 160-170.

Bolwig, N. (1959) A study of the nests built by mountain gorilla and chimpanzee. South African Journal of Science 55: 286-291.

Bourliere, F. (1979) Significant parameters of environmental quality for nonhuman primates. In: Bernstein, I.S. & Smith, E.O. (eds.) Primate Ecology & Human Origins: Ecological Influences on Social Organisation, Garland STPM Press, New York, pp.23-46.

Bourliere, F (1985) Primate communities: their structure and role in tropical ecosystems. International Journal of Primatology 6: 1-26.

Boyd Eaton, S. & Konner, M. (1985) Paleolithic nutrition, a consideration of its nature and current implications. New England Journal of Medicine 312: 283-289.

Brambell, M.R. (1972) Mammals: their nutrition and habit. In: T-W-Fiennes, R.N. (ed.) Biology of Nutrition, International Encyclopedia of Food and Nutrition 18: 613-648.

Brokaw, N.V.L. (1985a) Gap-phase regeneration in a tropical forest. Ecology 66: 682-687.

Brokaw, N.V.L. (1985b) Treefalls, regrowth, and community structure in tropical forests. In: Pickett, S.T.A. & White, P.S. (eds.) The Ecology of Natural Disturbance & Patch Dynamics, Academic Press, London, pp.53-69.

Brunig, E.F. (1983) Vegetation structure and growth. In: Golley, F.B. (ed.) Tropical Rain Forest Ecosystems. Stucture and Function, Elsevier Scientific Publishing Co., Amsterdam, pp.49-75.

Bullock, S.A. (1981) Dynamics of vegetative shoots of three species of Aframomum (Zingiberaceae) in Cameroon. Adansonia 20: 383-392.

Butynski, T.M. (1985) Primates and their conservation in the Impenetrable (Bwindi) Forest, Uganda. Primate Conservation 6: 68-72.

Butzler, W. (1980) Presence et repartition des gorilles, Gorilla gorilla gorilla (Savage and Wyman, 1847) au Cameroun. Saugetierkundliche Mitteilungen 28: 69-79.

Caballe, G. (1978) Essai sur la geographie forestiere du Gabon. Adansonia 17: 425-440.

Caballe, G. (1983) Vegetation. In: Barret, J. (ed.) Geographie et Cartographie du Gabon, EDICEF, Paris, pp.34-37.

Caballe G. & Fontes, J. (1978) Les inventaires forestiers au Gabon: applications a la phytogeographie. Bois et Forets des Tropiques 177: 15-33.

Calvert, J. (1985) Food selection by western gorillas in relation to food chemistry and selective logging in Cameroon, West Africa. PhD Thesis, University of California.

Caro, T.M. (1976) Observations on the ranging behaviour and daily activity of lone silverback mountain gorillas (Gorilla gorilla beringei). Animal Behaviour 24: 889-897.

Carroll, R.W. (1986) Status of the lowland gorilla and other wildlife in the Dzanga-Sanga region of southwestern Central African Republic. Primate Conservation 7: 38-41.

Casimir, M.J. (1975) Feeding ecology and nutrition of an eastern gorilla group in the Mt. Kahuzi region. Folia Primatologica 24: 81-136.

Casimir, M.J. (1979) An analysis of gorilla nesting sites of the Mt. Kahuzi region, (Zaire). Folia Primatologica 32: 290-305.

Casimir, M.J. & Butenandt, E. (1973) Migration and core area shifting in relation to some ecological factors in a mountain gorilla group, (Gorilla gorilla beringei), in the Mt. Kahuzi region. Zeitschrift fuer Tierspsychologie 33: 514-522.

Chapman, C.A. (1983) Speciation of tropical rainforest primates of Africa: insular biogeography. African Journal of Ecology 21: 297-308.

Chivers, D.J. & Hladik, C.M. (1980) Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. Journal of Morphology 166: 337-386.

Chivers, D.J. & Hladik, C.M. (1984) Diet and morphology in primates. In: Chivers, D.J., Wood, B.A. & Bilsborough, A. (eds.) Food Acquisition & Processing in Primates, Plenum Press, London, pp.213-230.

Clutton-Brock, T.H. & Harvey, P.H. (1977a) Primate ecology and social organisation. Journal of Zoology (London) 183: 1-39.

Clutton-Brock, T.H. & Harvey, P.H. (1977b) Species differences in feeding and ranging behaviour in primates. In: Clutton-Brock, T.H. (ed.) Primate Ecology, Academic Press, London pp.557-584.

Clutton-Brock, T.H. & Harvey, P.H. (1979) Home range size, population density and phylogeny in primates. In: Bernstein, I.S. & Smith, E.O. (eds.) Primate Ecology and Human Origins: Ecological Influences on Social Organisation, Gartland STPM Press, New York, pp.201-214.

Clutton-Brock, T.H. & Harvey, P.H. (1980) Primates, brains and ecology. Journal of Zoology 190: 309-323.

Collet, J-Y., Bourreau, E., Cooper, R.W., Tutin, C.E.G. & Fernandez, M. (1984) Experimental demonstration of cellulose digestion by Troglodytella gorillae, an intestinal ciliate of lowland gorillas. International Journal of Primatology 5: 328 (abstract).

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. Science 199: 1302-1309.

Coolidge, H.J (1929) A revision of the genus Gorilla. Memoirs of the Museum of Comparative Zoology, Harvard 50: 291-381.

Cousins, D. (1978a) Man's exploitation of the gorilla. Biological Conservation 13: 287-297.

Cousins, D. (1978b) The reaction of apes to water. International Zoo News 25: 8-13.

Cousins, D. (1982) Remarks on social status and racial variations in the gorilla in correlation with ecological changes. Unpublished manuscript.

Cousins, D. (1983) Man's affiliation with the anthropoid apes in Africa. Acta Zoologica et Pathologica Antverpiensia 77: 19-40.

Critchley, W. (1968) Report of the Takamanda gorilla survey. Unpublished manuscript.

Croat, T.B. (1975) Phenological behaviour of habit and habitat classes on Barro Colorado Island. Biotropica 7: 270-277.

Dasen, P.R. (1975) Concrete operational development in three cultures. Journal of Cross-Cultural Psychology 6: 156-172.

Davies, A.G. (1984) An ecological study of the red leaf monkey (Presbytis rubicunda) in the dipterocarp forest of northern Borneo. PhD Thesis, University of Cambridge.

Demment, M.W. (1983) Feeding ecology and the evolution of body size of baboons. African Journal of Ecology 24: 219-233.

Derscheid, J.M. (1927) Notes sur les gorilles des volcans du Kivu (Parc National Albert). Annales de la Societe Royale Zoologique de Belgique 58: 149-159.

Derochette, M. (1941) Les gorilles en territoire de Shabunda. Bulletin de la Societe de Botanique et de Zoologie Congolaises 4: 7-9.

Dixson, A.F. (1981) The Natural History of the Gorilla, Weidenfeld & Nicholson, London.

Donisthorpe, J.H. (1958) A pilot study of the mountain gorilla (Gorilla gorilla beringei) in South West Uganda, February to September 1957. South African Journal of Science 54: 195-217.

Douglas-Hamilton, I. & Douglas-Hamilton, O. (1975) Among the Elephants, Viking Press, New York.

Dubost, G. (1979) The size of African forest artiodactyls as determined by the vegetation structure. African Journal of Ecology 17: 1-17.

Dubost, G. (1984) Comparison of the diets of frugivorous forest ruminants of Gabon. Journal of Mammalogy 65: 298-316.

Du Chaillu, P.B. (1861) Explorations and Adventures in Equatorial Africa, John Murray, London.

Dunbar, R.I.M. (1987) Habitat quality, population dynamics, and group composition in colobus monkeys (Colobus guereza). International Journal of Primatology 8: 299-329.

Dunbar, R.I.M. (1988) Primate Social Systems, Croom Helm, London.

Dyce Sharpe, N.A. (1927) Notes on the gorilla. Proceedings of the Zoological Society of London 97: 1006-1009.

Eggeling, W.J. (1947) Observations on the ecology of the Budongo rain forest, Uganda. Journal of Ecology 34: 20-86.

Eisenberg, J.F., Muckenhirn, N.A. & Rudran, R. (1979) The relations between ecology and social structure in primates. In: Sussman, R.W. Primate Ecology: Problem-Orientated Field Studies, Wiley & Sons, New York, pp.455-484.

Elliot, R.C. (1976) Observations on a small group of mountain gorillas (Gorilla gorilla beringei). Folia Primatologica 25: 12-24.

Emlen, J.T. & Schaller, G.B. (1960) Distribution and status of the mountain gorilla (Gorilla gorilla beringei) - 1959. Zoologica 45: 41-52.

Emmons, L.H., Gautier-Hion, A. & Dubost, G. (1983) Community structure of the frugivorous-folivorous forest mammals of Gabon. Journal of Zoology 199: 209-222.

Estrada, A. & Coates-Estrada, R. (1984) Fruit eating and seed dispersal by howling monkeys (Alouatta palliata) in the tropical rain forest of Los Tuxtlas, Mexico. American Journal of Primatology 6: 77-91.

Estrada, A. & Coates-Estrada, R. (1986) Frugivory in howling monkeys (Alouatta palliata) at Los Tuxtlas, Mexico: dispersal and fate of seeds. In: Estrada, A. & Fleming, T.H. (eds.) Frugivores & Seed Dispersal, Junk Publishers, The Netherlands, pp.93-104.

Fleming, T.H. (1979) Do tropical frugivores compete for food? American Zoologist 19: 1157-1172.

Florence, J. (1981) Chablis et sylvigenese dans une foret dense humide sempervirente du Gabon. PhD Thesis, University of Strasbourg.

Foose, T.J., Seal, U.S. & Flesness, N.R. (1987) Captive propagation as a component of conservation strategies for endangered primates. In: Marsh, C.W. & Mittermeier, R.A. (eds.) Primate Conservation in the Tropical Rain Forest, Alan R. Liss, New York, pp.263-299.

Fossey, D. (1972) Vocalisation of mountain gorilla (Gorilla gorilla beringei). Animal Behaviour 20: 36-53.

Fossey, D. (1974) Observations on the home range of one group of mountain gorillas (Gorilla gorilla beringei). Animal Behaviour 22: 568-581.

Fossey, D. (1976) The behaviour of the mountain gorilla. PhD Thesis, University of Cambridge.

Fossey, D. (1979) Development of the mountain gorilla (Gorilla gorilla beringei): the first thirty six months. In: Hamburg, D.A. & McCown, E.R. (eds.) The Great Apes, Benjamin/Cummings, London, pp.139-184.

Fossey, D. (1983) Gorillas in the Mist, Houghton Mifflin, Boston.

Fossey, D. (1984) Infanticide in mountain gorillas (Gorilla gorilla beringei) with comparative notes on on chimpanzees. In: Hausfater, G. & Hrdy, S.B. (eds.) Infanticide: Comparative and Evolutionary Perspectives, Aldine Pub., New York, pp.217-235.

Fossey, D. & Harcourt, A.H. (1977) Feeding ecology of free-ranging mountain gorilla (Gorilla gorilla beringei). In: Clutton-Brock, T.H. (ed.) Primate Ecology, Academic Press, London, pp.415-447.

Foster, R.B. (1982a) The seasonal rhythm of fruit fall on Barro Colorado Island. In: Leigh, E.G., Rand, A.S. & Windsor, D.M. (eds.) The Ecology of a Tropical Forest: Seasonal Rhythms & Long Term Changes. Smithsonian Institution Press, Washington D.C., pp.151-172.

Foster, R.B. (1982b) Famine on Barro Colorado Island. In: Leigh, E.G., Rand, A.S. & Windsor, D.M. (eds.) The Ecology of a Tropical Forest: Seasonal Rhythms & Long Term Changes, Smithsonian Institution Press, Washington D.C., pp.201-212.

Galdikas, B.M.F. (1979) Orangutan adaptions at Tanjung Puting reserve: Mating and ecology. In: Hamburg, D.A. & McCown, E.R. (eds.) The Great Apes, Benjamin/Cummings, London, pp.195-234.

Galdikas, B.M.F. (1981) Wild orangutan studies at Tanjung Puting Reserve, central Indonesian Borneo, 1971-1977. National Geographic Research Reports 13: 1-10.

Galdikas, B.M.F. (1982) Orang-utans as seed-dispersers at Tanjung Puting, central Kalimantan: implications for conservation. In: Boer, L.E.M. de (ed.) The Orang Utan, Its Biology & Conservation, Boston Hingam, The Hague, pp.285-298.

Ganzhorn, J.U. (1987) Soil consumption of two groups of semi-free-ranging lemurs (Lemur catta and Lemur fulvus). Ethology 74: 146-154.

Garber, P.A. (1986) The ecology of seed dispersal in two species of Callitrichid primates (Saguinus mystax and Saguinus fuscicollis). American Journal of Primatology 10: 155-170.

Garber, P.A. (1987) Foraging strategies among living primates. Annual Review of Anthropology 16: 339-364.

Garin, Y., Tutin, C.E.G., Fernandez, M. & Goussard, B. (1982) A new intestinal parasitic entodiniomorph ciliate from wild lowland gorillas (Gorilla gorilla gorilla) in Gabon? Journal of Medical Primatology 11: 186-190.

Garner, R.L. (1896) Gorillas & Chimpanzees, Harpers, London.

Garner, R.L. (1919) Apes and men. The Independent 99: 400-401.

Garner, R.L. (1920) Contemporary Ancestors of Ours. The Independent 101: 60-61 & 70.

Gartlan, J.S. (1980) Western gorillas. Unpublished manuscript.

Gartlan, J.S. & Strusaker, T.T. (1972) Polyspecific associations and niche separations of rain forest anthropoids in Cameroon, West Africa. Journal of Zoology (London) 168: 221-266.

Gartlan, J.S., McKey, D.B. & Waterman, P.G. (1978) Soils, forest structure and feeding behaviour of primates in a Cameroon coastal forest. In: Chivers, D.J. & Herbert, J. (eds.) Recent Advances in Primatology Volume 1, Academic Press, London, pp.259-267.

Gaulin, S.J.C. (1979) A Jarman/Bell model of primate feeding niches. Human Ecology 7: 1-20.

Gautier-Hion, A. (1971) L'ecologie du talapoin du Gabon. La Terre et la Vie 25: 427-490.

Gautier-Hion, A. (1978) Food niche and coexistence in sympatric primates in Gabon. In: Chivers, D.J. & Herbert, J. (eds.) Recent Advances in Primatology Volume 1, Academic Press, London, pp.269-286.

Gautier-Hion, A. (1980) Seasonal variations of diet related to species and sex in a community of Cercopithecus monkeys. Journal of Animal Ecology 49: 237-269.

Gautier-Hion, A. (1983) Leaf consumption by monkeys in western and eastern Africa: a comparison. African Journal of Ecology 21: 107-113.

Gautier-Hion, A. (1984) La dissemination des graines par les cercopithecides forestier Africains. Revue d'Ecologie (Terre et Vie) 39: 159-165.

Gautier-Hion, A., Emmons, L.H. & Dubost, G. (1980) A comparison of the diets of three major groups of primary consumers of Gabon (primates, squirrels and ruminants). Oecologia 45: 182-189.

Gautier-Hion, A., Gautier, J-P. & Quris, R. (1981) Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys Cercopithecus cephus. Revue d'Ecologie (Terre et Vie) 35: 511-536.

Gautier-Hion, A., Duplantier, J-M., Emmons, L., Feer, F., Hecketsweiler, P., Moungazi, A., Quris, R. & Sourd, C. (1985a) Coadaption entre rythmes de fructification et frugivore en foret tropicale humide du Gabon: mythe ou realite. Revue d'Ecologie (Terre et Vie) 40: 405-434.

Gautier-Hion, A., Duplantier, J-M., Quris, R., Feer, F., Sourd, C., Decoux, J-P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J-M. (1985b) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65: 324-337.

Ghiglieri, M.P. (1984a) The Chimpanzees of Kibale Forest: a Field Study of Ecology & Social Structure, Columbia University Press, New York.

Ghiglieri, M.P. (1984b) Feeding ecology and sociality of chimpanzees in Kibale forest, Uganda. In: Rodman, P.S. & Cant, J.G.H. (eds.) Adaptions for Foraging in Nonhuman Primates, Columbia University Press, New York, pp.161-194.

Ghiglieri, M.P. (1987) Sociobiology of great apes and the hominid ancestor. Journal of Human Evolution 16: 319-357.

Glander, K.E. (1975) Habitat description and resource utilization: a preliminary report on mantled howling monkey ecology. In: Tuttle, R.H. (ed.) Socioecology & Psychology of Primates, Mouton, The Hague, pp.37-57.

Glander, K.E. (1981) Feeding patterns in mantled howling monkeys. In: Kamil, A.C. & Sargent, T.D. (eds.) Foraging Behavior: Ecological, Ethological, and Psychological Approaches, Garland STPM Press, New York, pp.231-257.

Golding, R.R. (1972) A gorilla and chimpanzee exhibit at the University of Ibadan zoo. International Zoo Yearbook 12: 71-76.

Goodall, A.G. (1974) Studies on the ecology of the mountain gorilla (Gorilla gorilla beringei) of the Mount Kahuzi-Biega region (Zaire) and comparisons with the mountain gorillas of the Virunga volcanoes. PhD Thesis, University of Liverpool.

Goodall, A.G. (1977) Feeding and ranging behaviour of a mountain gorilla group (Gorilla gorilla beringei) in the Tshinda-Kahuzi region (Zaire). In: Clutton-Brock, T.H. (ed.) Primate Ecology, Academic Press, London, pp.449-479.

Goodall, A.G. & Groves, C.P. (1977) The conservation of eastern gorillas. In: Rainer, H.R.H. & Bourne, G.H. (eds.) Primate Conservation, Academic Press, London, pp.599-637.

Goodall, J. (1962) Nest building behavior in the free ranging chimpanzee. Annals of the New York Academy of Science 102: 455-67.

Goodall, J. van Lawick (1968) The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Animal Behaviour Monographs 1: 161-311.

Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., Pierce, A. & Riss, D. (1979) Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: Hamburg, D.A. & McCown, E.R. (eds.) The Great Apes, Benjamin/ Cummings, London, pp.13-53.

Gray, J.E. (1861) Observations on Mr. Du Chaillu's papers on "The New Species of Mammals" discovered by him in western Equatorial Africa. Proceedings of the Zoological Society (London) 18: 273-278.

Groves, C.P. (1967) Ecology and taxonomy of the gorilla. Nature 213: 890-893.

Groves, C.P. (1970a) Population systematics of the gorilla. Journal of Zoology (London) 161: 287-300.

Groves, C.P. (1970b) Gigantopithecus and the mountain gorilla. Nature 226: 973-974.

Groves, C.P. (1971) Distribution and place of origin of the gorilla. Man 6: 44-51.

Groves, C.P. (1986) Systematics of the great apes. In: Swindler, D.R. & Erwin, J. (eds.) Comparative Primate Biology Volume 1: Systematics, Evolution, & Anatomy, Alan R. Liss, New York, pp.187-217.

Groves, C.P. & Humphrey, N.K. (1973) Asymmetry in gorilla skulls: evidence of lateralised brain function? Nature 244: 53-54.

Groves, C.P. & Napier, J.R. (1966) Skulls and skeletons of Gorilla in British collections. Journal of Zoology 148: 153-161.

Groves, C.P. & Sabater Pi, J. (1985) From ape's nest to human fixpoint. Man 20: 22-47.

Groves, C.P. & Stott, K.W. (1979) Systematic relationships of gorillas from Kahuzi, Tshiaberimu, and Kayonza. Folia Primatologica 32: 161-179.

Halle, N. (1987) Cola Lizae N.Halle (Sterculiaceae) Nouvelle espece du Moyen Ogooue (Gabon). Adansonia 3: 229-237.

Halle, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978) Tropical Trees and Forests: An Architectural Analysis, Springer-Verlag, Berlin.

Hancocks, D. (1983) Gorillas go natural. Animal Kingdom 86: 10-16.

Harcourt, A.H. (1978) Strategies of emigration and transfer by primates, with particular reference to gorillas. Zeitschrift fuer Tierpsychologie 48: 401-420.

Harcourt, A.H. (1979) The social relationships and group structure of wild mountain gorillas. In: Hamburg, D.A. & McCown, E.R. (eds.) The Great Apes. Benjamin/Cummings, London, pp.187-192.

Harcourt, A.H. & Harcourt, S.A. (1984) Insectivory by gorillas. Folia Primatologica 43: 229-233.

Harcourt, A.H. & Stewart, K.J. (1980) Gorilla-eaters of Gabon. Oryx 15: 248-251.

Harcourt, A.H. & Stewart, K.J. (1984) Gorillas' time feeding: aspects of methodology, body size, competition and diet. African Journal of Ecology 22: 207-215.

Harcourt, A.H., Fossey, D. & Sabater Pi, J. (1981) Demography of Gorilla gorilla. Journal of Zoology 195: 215-233.

Harcourt, A.H., Stewart, K.J. & Harcourt, D.E. (1986) Vocalisation and social relations of wild gorillas: a preliminary analysis. In: Taub, D.M. & King, F.A. (eds.) Current Perspectives in Primate Social Dynamics, Van Nostrand Reinhold Co, New York, pp.346-356.

Harcourt, A.H., Stewart, K.J. & Inahoro, I.M. (1988) Conservation status of gorillas in Nigeria. Primate Eye 35: 26-27.

Harrison, M.J.S. (1983) Patterns of range use by the green monkey, Cercopithecus sabaeus at Mt. Assirik, Senegal. Folia Primatologica 41: 157-179.

Harrison, M.J.S. (1984) The ecology of black colobus monkeys Colobus satanus in Gabon. Unpublished report.

Harrison, M.J.S. (1988) A new species of guenon (genus Cercopithecus) from Gabon. Journal of Zoology, London 215: 561-575.

Harrison, M.J.S. & Hladik, C.M. (1986) Un primate granivore: le colobe noir dans la foret du Gabon; potentialite d'evolution du comportement alimentaire. Revue d'Ecologie (Terre et Vie) 41: 281-298.

Hartmann, R. (1885) Anthropoid Apes, Kegan Paul, London.

Hartshorn, G.S. (1978) Tree falls and tropical forest dynamics. In: Tomlinson, P.B. & Zimmerman, M.H. (eds.) Tropical Trees as Living Systems, Cambridge University Press, Cambridge, pp.671-638.

Hartshorn, G.S. (1980) Neotropical forest dynamics. Biotropica (suppl.) 12: 23-30.

Harvey, P.H. & Clutton-Brock, T.H. (1981) Primate home-range size and metabolic needs. Behavioural Ecology and Sociobiology 8: 151-155.

Harvey, P.H. & Clutton-Brock, T.H. (1983) The survival of a theory. New Scientist 98: 313-315.

Harvey, P.H., Clutton-Brock, T.H. & Mace, G.M. (1980) Brain size and ecology in small mammals and primates. Proceedings of the National Academy of Science (USA) 77: 4387-4389.

Hausfater G. & Meade, B.J. (1982) Alternation of sleeping groves by yellow baboons (Papio cephalus) as a stategy for parasite avoidance. Primates 23: 287-297.

Hediger, H.P (1977) Nest and home. Folia Primatologica 28: 170-187.

Herrera, C.M. (1981) Are tropical fruits more rewarding to dispersers than temperate ones? American Naturalist 118: 896-907.

Herrera, C.M. (1982) Defence of ripe fruits from pests: its significance in relation to plant-disperser interactions. American Naturalist 120: 218-241.

Hill, M.O. (1979) TWINSPAN - a fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes, Cornell University, New York.

Hladik, A. (1978) Phenology of leaf production in rain forest of Gabon: distribution and composition of food for folivores. In: Montgomery, G.G. (ed.) The Ecology of Arboreal Folivores, Smithsonian Institution Press, Washington D.C., pp.51-71.

Hladik, A. (1982) Dynamique d'une foret equatoriale africaine: mesures en temps reel et comparaison du potentiel de croissance des differentes especes. Acta Ocecologia 3: 373-392.

Hladik, A. (1984) The information on tropical forest dynamics as given by basal area measurements. In: Agren, G.I. (ed.) State and Change of Forest Ecosystems - Indicators in Current Research, Swedish University Agricultural Science Department, Ecology & Environmental Research Report 13:

Hladik, A. & Halle, N. (1973) Catalogue des phanerogames du Nord-Est du Gabon (5e liste). Adansonia 13: 527-544.

Hladik, C.M. (1967) Surface relatif du tractus digestif de quelques primates, morphologie de villosites intestinales et correlations avec le regime alimentaire. Mammalia 31: 120-147.

Hladik, C.M. (1973) Alimentation et activite d'un groupe de chimpanzes reintroduits en foret Gabonaise. La Terre et la Vie 27: 343-413.

Hladik, C.M. (1977) Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet. In: Clutton-Brock, T.H. (ed.) Primate Ecology, Academic Press, London, pp.481-501.

Hladik, C.M. (1981) Diet and evolution of feeding strategies among forest primates. In: Harding, R.S.O. & Teleki, G. (eds.) Omnivorous Primates: Gathering & Hunting in Human Evolution, Columbia University Press, New York, pp.215-254.

Hladik, C.M. & Chivers, D.J. (1978) Ecological factors and specific behavioural patterns determining primate diet. In: Chivers, D.J. & Herbert, J. (eds.) Recent Advances in Primatology Volume 1, Academic Press, London, pp.433-444.

Hladik, C.M. & Gueguen, L. (1974) Geophagie et nutrition minerale chez les primates sauvages. Comptes Rendus de l'Academie des Sciences Paris, Serie D 279: 1393-1396.

Hladik, C.M. & Viroben, G. (1974) L'alimentation proteique du chimpanze dans son environment forestier naturel. Comptes Rendus de L'Academie des Sciences, Paris, Serie D 279: 1475-1478.

Hopkins, B. (1970) Vegetation of the Olokemeji Forest Reserve, Nigeria. Journal of Ecology 58: 765-795.

Hoshino, J. (1985) Feeding ecology of mandrills (Mandrillus sphinx) in Campo Animal Reserve, Cameroon. Primates 26: 248-273.

Howe, H.F. (1980) Monkey dispersal and waste of a neotropical fruit. Ecology 61: 944-959.

Hubbell, S.P. & Foster, R. (1983) Diversity of canopy trees in a neotropical forest and implications for conservation. In: Sutton, S.L., Whitmore, T.C. & Chadwick, A.C. (eds.) Tropical Rain Forest: Ecology and Management, Blackwell, Oxford, pp.25-41.

Hubbell, S.P & Foster, R.B. (1986) Biology, chance, and history and the structure of tropical rain forest tree communities. In: Diamond, J. & Case, T.J. (eds.) Community Ecology, Harper & Row, New York, pp.314-329.

Hylander, W.L. (1975) Incisor size and diet in anthropoids with special reference to Cercopithecoidea. Science 189: 1095-1098.

Hylander, W.L. (1979) The functional significance of primate mandibular form. Journal of Morphology 160: 223-240.

Idani, G. (1986) Seed dispersal by pygmy chimpanzees (Pan paniscus): a preliminary report. Primates 27: 441-447.

Ischac, P. (1938) Les gorilles. La Nature 3025: 300-305.

IUCN (1988) Threatened Primates in Africa. The IUCN Red Data Book. (Compiled by Lee, P., Thornback, J. & Bennet, E.L.), IUCN Conservation Monitoring Centre, Cambridge.

Janzen, D.H. (1978) Complications in interpreting the chemical defences of trees against tropical arboreal plant-eating vertebrates. In: Montgomery, G.G. (ed.) The Ecology of Arboreal Folivores, Smithsonian Institution Press, Washington D.C., pp.73-84.

Jenks, A.E. (1911) Bulu knowledge of the gorilla and chimpanzee. American Anthropologist 13: 56-64.

Johns, A.D. (1986) Effects of selective logging on the behavioural ecology of West Malaysian primates. Ecology 67: 684-694.

Jones, C. & Sabater Pi, J. (1971) Comparative ecology of Gorilla gorilla (Savage & Wyman) and Pan trogodytes (Blumenbach) in Rio Muni, West Africa. Bibliotheca Primatologica 13: 1-96.

IPN (1983) (Institut Pedagogique National et Laboratoire National de Cartographie) Climatologie. In: Barret, J. (ed.) Geographie et Cartographie du Gabon, EDICEF, Paris, pp.22-25.

Kano, T. (1982) The use of leafy twigs for rain cover by the pygmy chimpanzees of Wamba. Primates 23: 453-457.

Kano, T. (1983) An ecological study of the pygmy chimpanzees (Pan paniscus) of Yalosidi, Republic of Zaire. International Journal of Primatology 4: 1-31.

Kano, T. & Mulavwa, M. (1984) Feeding ecology of the pygmy chimps (Pan paniscus) of Wamba. In: Susman, R.L (ed.) The Pygmy Chimpanzee. Evolutionary Biology & Behavior, Plenum Press, London, pp.233-274.

Kawai, M. & Misuhara, H. (1959) An ecological study of the wild mountain gorilla (Gorilla gorilla beringei) - a report of the Japan monkey centre 2nd gorilla expedition 1959. Primates 2: 1-42.

Kay, R.F. (1975) The functional adaptions of primate molar teeth. American Journal of Physical Anthropology 43: 195-215.

Kay, R.F. (1977) Diets of early Miocene African hominoids. Nature 268: 628-630.

Kay, R.F. (1981) The nut-crackers: a new theory of the adaptions of the Ramapithecinae. American Journal of Physical Anthropology 55: 141-152.

Kay, R.F. (1984) On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman, P.S. & Cant, J.G.H. (eds.) Adaptions for Foraging in Nonhuman Primates, Columbia University Press, New York, pp.21-53.

Kay, R.F. & Covert, H.H. (1984) Anatomy and behaviour of extinct primates. In: Chivers, D.J., Wood, B.A. & Bilsborough, A. (eds.) Food Acquisition & Processing in Primates, Plenum Press, London, pp.467-508.

Kay, R.F. & Hylander, W.L. (1978) The dental structure of mammalian folivores with special reference to primates and phalangeroidea (Marsupialia). In: Montgomery, G.G. (ed.) The Ecology of Arboreal Folivores, Smithsonian Institution Press, Washington D.C., pp.173-191.

Keith, A. (1896) An introduction to the study of anthropoid apes, I. The gorilla. Natural Science (London) 9: 26-37.

Kershaw, K.A. & Looney, J.H. (1985) Quantitative and Dynamic Plant Ecology, 3rd Edition, Edward Arnold, London.

Kinzey, W.G. (1974) Ceboid models for the evolution of hominoid dentition. Journal of Human Evolution 3: 193-203.

Kinzey, W.G. (1984) The dentition of the pygmy chimpanzee, Pan paniscus. In: Susman, R.L (ed.) The Pygmy Chimpanzee. Evolutionary Biology & Behavior. Plenum Press, London, pp.65-88.

Kitamura, K. (1983) Pygmy chimpanzee association patterns in ranging. Primates 24: 1-12.

Knight, D.H. (1975) An analysis of late secondary succession in species-rich tropical forest. In: Golley, F.B. & Medina, E. (eds.) Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research, Ecological Studies Vol. II, Springer-Verlag, New York, pp.53-59.

Kohler, W. (1927) The Mentality of Apes, 2nd Edition, Keagan Paul, London.

Kortlandt, A. (1972) New Perspectives on Ape and Human Evolution, Stichting voor Psychobiologie, Amsterdam.

Kortlandt, A. (1984) Vegetation research and the "bulldozer" herbivores of tropical Africa. In: Chadwick, A.C. & Sutton, S.L. (eds.) Tropical Rain-Forest: The Leeds Symposium, Blackwell, Oxford, pp.205-226.

Kurland, J.A. & Gaulin, S.J.C. (1987) Comparability among measures of primate diets. Primates 28: 71-77.

Lahm, S.A. (1986) Diet and habitat preference of Mandillus sphinx in Gabon: implications of foraging strategy. American Journal of Primatology 11: 9-26.

Laws, R.M. (1970) Elephants as agents of habitat and landscape changes in east Africa. Oikos 21: 1-15.

Ledoux, A. (1950) Recherche sur la biologie de la fourmi fileuse (Oecophylla longinoda Latr.). Annales des Sciences Naturelles de Zoologie 11e serie 12: 313-461.

Leigh, E.G., Jr. (1975) Structure and climate in tropical rain forest. Annual Review of Ecology & Systematics 6: 67-86.

Leigh, E.G., Jr. (1982) Introduction. In: Leigh, E.G., Rand, A.S. & Windsor, D.M. (eds.) The Ecology of a Tropical Forest: Seasonal Rhythms & Long Term Changes, Smithsonian Institution Press, Washington D.C., pp.11-18.

Leighton, M. & Leighton, D.R. (1983) Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton, S.L., Whitmore, T.C. & Chadwick, A.C. (eds.) Tropical Rain Forest: Ecology and Management, Blackwell, Oxford, pp.181-196.

Lethmate, J. (1977) Nestbauverhalten eines isoliert aufgezogenen, jungen Orang Utans, Primates 18: 545-554.

Lewis, D.M. (1987) Fruiting patterns, seed germination, and distribution of Sclerocarya caffra in an elephant-inhabited woodland. Biotropica 19: 50-56.

Lieberman, D. (1982) Seasonality and phenology in a dry tropical forest in Ghana. Journal of Ecology 70: 791-806.

Lieberman, D., Lieberman, M. & Martin, C. (1987) Notes on seeds in elephant dung from Bia National Park, Ghana. Biotropica 19: 365-369.

Lieberman, M. & Lieberman, D. (1986) An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. Journal of Tropical Ecology 2: 113-126.

Liz Ferreira, A.J. de, Athayde, A. & Magalhaes, H. de (1945) Gorilas do Maiombe Portugues. Junta das Missoes Geograficas e de Investigacoes Coloniais. Memorias 1: 1-159.

MacKinnon, J. (1974) The behaviour and ecology of wild orang-utans (Pongo pygmaeus). Animal Behaviour 22: 3-74.

Malbrant, R. & Maclatchy, A. (1949) Faune de l'Equateur Africain Francais. Tome II. Mammiferes, Paul Chechevalier, Paris.

Maple, T.L. & Hoff, M.P. (1982) Gorilla Behaviour, Van Nostrand Reinhold, New York.

March, E.W. (1957) Gorillas of Eastern Nigeria. Oryx 4: 30-34.

Marler, P. (1976) Social organisation, communication and graded signals: the chimpanzee and the gorilla. In: Bateson, P.P.G. & Hinde, R.A. (eds.) Growing Points in Ethology, Cambridge University Press, Cambridge, pp.239-280.

Marler, P. & Tenaza, R. (1977) Signalling behaviour of apes with special reference to vocalization. In: Sebeok, T.A. (ed.) How Animals Communicate, Bloomington, Indiana University Press, pp.965-1033.

Martin, L. (1985) Significance of enamel thickness in hominoid evolution. Nature 314: 260-263.

Martin, R.D. (1984) Body size, brain size and feeding strategies. In: Chivers, D.J., Wood, B.A. & Bilsborough, A. (eds.) Food Acquisition & Processing in Primates, Plenum Press, London, pp.73-103.

Martin, R.D., Chivers, D.J, MacLarnon, A.M. & Hladik, C.M. (1985) Gastrointestinal allometry in primates and other mammals. In: Jungers, W.L. (ed.) Size & Scaling in Primate Biology, Plenum Press, New York, pp. 61-90.

Maryanski, A.R. (1987) African ape social structure: is there strength in weak ties? Social Networks 9: 191-215.

Maunder, S. (1885) The Treasury of Natural History, Longmans & Co., London.

Maxwell, M. (1928) The home of the eastern gorilla. Journal of the Bombay Natural History Society 32: 436-449.

McGrew, W.C. (1983) Animal foods in the diets of wild chimpanzees (Pan troglodytes): why cross-cultural variation. Journal of Ethology 1: 46-61.

Menzel, E.W. (1973) Chimpanzee spatial memory organisation. Science 182: 943-945.

Merfield, F.G. (1954) The gorilla of the French Cameroons. Zoo Life 9: 84-94.

Merfield, F.G. (1956) Gorillas Were My Neighbours, Longmans, London.

Milton, K. (1979) Factors influencing leaf choice by howler monkeys: a test for some hypotheses of food selection by generalist herbivores. American Naturalist 114: 362-377.

Milton, K. (1980) The Foraging Strategy of Howler Monkeys. Columbia University Press, New York.

Milton, K. (1981a) Food choice and digestive strategies of two sympatric primate species. American Naturalist 117: 496-505.

Milton, K. (1981b) Distribution patterns of tropical plants as an evolutionary stimulus to primate mental development. American Anthropologist 83: 534-548.

Milton, K. (1982) Dietary quality and demographic regulation in a howler monkey population. In: Leigh, E.G., Rand, A.S. & Windsor, D.M. (eds.) The Ecology of a Tropical Forest: Seasonal Rhythms & Long Term Changes. Smithsonian Institution Press, Washington D.C., pp.273-289.

Milton, K. (1984) The role of food-processing factors in primate food choice. In: Rodman, P.S. & Cant, J.G.H. (eds.) Adaptions for Foraging in Nonhuman Primates, Columbia University Press, New York, pp.249-279.

Milton, K. (1986) Digestive physiology in primates. NIPS 1: 76-79.

Milton, K. (1987) Primates diets and gut morphology: implications for hominid evolution. In: Harris, M. & Ross, E.B. (eds.) Food & Evolution: Towards a Theory of Human Diets, Temple University Press, Philadelphia, pp.93-115.

Milton, K. & May, M.L. (1976) Body weight, diet and home range area in primates. Nature 259: 459-462.

Milton, K., Windsor, D.M. & Morrison, D.W. (1982) Fruiting phenologies of two neotropical Ficus species. Ecology 63: 752-762.

Mittermeier, R. & Oates, J.F. (1985) Primate diversity: the world's top countries. Primate Conservation 5: 41-46.

Moreno-Black, G. (1978) The use of scat samples in primate diet analysis. Primates 19: 215-221.

Mori, A. (1983) Comparison of the communicative vocalizations and behaviors of group ranging in eastern gorillas, chimpanzees and pygmy chimpanzees. Primates 24: 486-500.

Napier, J. (1963) Brachiation and brachiators. Symposia of the Zoological Society of London 10: 183-195.

Nicholl, M. & Langrand, O. (1986) Conservation et utilisation rationelle des ecosystemes forestiere du Gabon. WWW/IUCN report no. 3247.

Nishida, T. (1976) The bark-eating habits in primates, with special reference to their to status in the diet of wild chimpanzees. Folia Primatologica 25: 277-287.

Nishida, T. (1979) The social structure of chimpanzees of the Mahale Mountains. In: Hamburg, D.A. & McCown, E.R. (eds.) The Great Apes, Benjamin/Cummings, London, pp.73-121.

Nishida, T. & Hiraiwa, M. (1982) Natural history of a tool-using behaviour by wild chimpanzees in feeding upon wood-boring ants. Journal of Human Evolution 11: 73-99.

Nishida, T. & Uehara, S. (1983) Natural diet of chimpanzees (Pan troglodytes schweinfurthii). Long-term records from the Mahale Mountains, Tanzania. African Study Monographs 3: 109-130.

Nissen, H.W. (1931) A field study of the chimpanzee. Observations of chimpanzee behavior. Observations of chimpanzee bahaviour and environment in Western French Guinea. Comparative Psychology Monographs 8: 1-122.

Oates, J.F. (1978) Water-plant and soil consumption by guereza monkeys (Colobus gueraza): a relationship with minerals and toxins in the diet? Biotropica 10: 241-253.

Oates, J.F., Waterman, P.G. & Choo, G.M. (1980) Food selection by the south Indian leaf-monkey, Presbytis johnii, in relation to leaf chemistry. Oecologia 45: 45-56.

Oates, J.F. (1986a) Action Plan for African Primate Conservation: 1986-1990, IUCN/SSC Primate Specialist Group, Stony Brook, New York.

Oates, J.F. (1986b) African primate conservation: general needs and specific priorities. In: Benirschke, K. (ed.) Primates: The Road to Self-Sustaining Populations, Springer-Verlag, New York, pp.21-29.

Oates, J.F., Gartlan, J.S. & Strusaker, T.T. (1987) A framework for African rain forest primate conservation. In: Marsh, C.W. & Mittermeier, R.A. (eds.) Primate Conservation in the Tropical Rain Forest, Alan R. Liss, New York, pp.321-327.

Oates, J.F., Swain, T. & Zantovska, J. (1977) Secondary compounds and food selection by Colobus monkeys. Biochemical Systematics & Ecology 5: 317-321.

Oates, J.F., Waterman, P.G. & Choo, G.M. (1980) Food selection by the south Indian leaf-monkey, Presbytis johnii, in relation to leaf chemistry. Oecologia 45: 45-56.

Olsen, D.K. (1986) Determining range size for arboreal monkeys: methods, assumptions and accuracy. In: Taub, D.M. & King, F.A. (eds.) Current Perspectives in Primate Social Dynamics, Van Nostrand Reinhold, New York, pp.212-227.

Opler, P.A., Frankie, G.W. & Baker, H.G. (1980) Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 68: 167-188.

Osborn, R.M. (1963) Observations on the behaviour of the mountain gorilla. Symposia of the Zoological Society of London 10: 29-37.

Patterson, T.L. & Tzeng, O.J.L. (1979) Long-term memory for abstract concepts in the lowland gorilla (Gorilla gorilla gorilla). Bulletin of the Psychonomic Society 13: 279-282.

Petit, L. (1920) Notes sur le gorille. Bulletin de la Societe Zoologique de France 45: 308-313.

Pielou, E.C. (1966) The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131-144.

Pierce, A.H. (1978) Ranging patterns and associatins of a small community of chimpanzees in Gombe National Park Tanzania. In: Chivers, D.J. & Herbert, J. (eds.) Recent Advances in Primatology Volume 1, Academic Press, London, pp.59-61.

Pitman, C.R.S. (1935) The gorillas of western Kigezi - South West Uganda. Proceedings of the Zoological Society of London 105: 477-99.

Putnam, R.J. (1984) Facts from faeces. Mammalian Review 14: 79-97.

Raemaekers, J. (1980) Causes of variation between months in the distance traveled by gibbons. Folia Primatalogica 34: 46-60.

Raemaekers, J.J., Aldrich-Blake, F.P.G. & Payne, J.B. (1980) The forest. In: Chivers, D.J. (ed.) Malayan Forest Primates, Plenum Press, London, pp.29-62.

Reade, W.W. (1863) Savage Africa, Elder & Co., London.

Redford, K.H. (1987) Ants and termites as food. Patterns of mammalian myrmecophagy. In: Genoways, H.H. (ed.) Current Mammalogy Volume 1, Plenum Press, New York, pp.349-399.

Reynolds, V. (1965) Some behavioural comparisons between the chimpanzee and the mountain gorilla in the wild. American Anthropology 67: 671-706.

Reynolds, V. (1967) The Apes, Cassell, London.

Reynolds, V. (1975) How wild are the Gombe chimpanzees? Man 10: 123-125.

Reynolds, V. & Reynolds, F. (1965) Chimpanzees of the Budongo Forest. In: DeVore, I. (ed.) Primate Behavior, Holt Rinehart & Winston, New York, pp.368-424.

Richard, A.F. (1985) Primates in Nature, Freeman, New York.

Richards, P.W. (1952) The Tropical Rain Forest, Cambridge University Press, Cambridge.

Richards, P.W. (1983) The three-dimensional structure of tropical rain forest. In: Sutton, S.L., Whitmore, T.C. & Chadwick, A.C. (eds.) Tropical Rain Forest: Ecology and Management, Blackwell, Oxford, pp.3-10.

Rijksen, H.D. (1978) A Fieldstudy on Sumatran Orang Utans (Pongo pymaeus abelii Lesson 1827) Ecology, Behaviour & Conservation, Veeman & Zonen, Wageningen, The Netherlands.

Rodman, P.S. (1977) Feeding behaviour of orang-utans of the Kutai Nature Reserve, East Kalimantan. In: Clutton-Brock, T.H. (ed.) Primate Ecology, Academic Press, London pp.383-413.

Rogers, M.E. & Williamson, E.A. (1987) Density of herbaceous plants eaten by gorillas in Gabon: some preliminary data. Biotropica 19: 278-281.

Rumbaugh, D.M. & Gill, T.V. (1973) The learning skills of great apes. Journal of Human Evolution 2: 171-179.

Rumiz, D.I., Zunino, G.E., Obregozo, M.L. & Ruiz, J.C. (1986) Alouatta caraya: habitat and resource utilization in northern Argentina. In: Taub, D.M. & King, F.A. (eds.) Current Perspectives in Primate Social Dynamics, Van Nostrand Reinhold, New York, pp.175-193.

Ryan, A.S. (1981) Anterior dental microwear and its relationship to diet and feeding behaviour in three African primates (Pan troglodytes troglodytes, Gorilla gorilla gorilla, Papio hamadryas). Primates 24: 533-550.

Sabater Pi, J. (1966a) Gorilla attacks against humans in Rio Muni, West Africa. Journal of Mammalogy 47: 123-124.

Sabater Pi, J. (1966b) Rapport preliminaire sur l'alimentation dans la nature des gorilles du Rio Muni (Ouest Africain). Mammalia 30: 235-240.

Sabater Pi, J. (1977) Contribution to the study of alimentation of lowland gorillas in the natural state, in Rio Muni, Republic of Equatorial Guinea (West Africa). Primates 18: 183-204.

Sabater Pi, J. (1981) Exploitation of gorillas Gorilla gorilla gorilla Savage & Wyman 1847 in Rio Muni, Republic of Equatorial Guinea, West Africa. Biological Conservation 19: 131-140.

Sabater Pi, J. & Groves, C. (1972) The importance of the higher primates in the diet of the Fang in Rio Muni. Man 7: 239-243.

Sabatier, D. (1985) Saisonnalite et determinism du pic de fructification en foret Guyanaise. Revue d'Ecologie (Terre et Vie) 40: 289-320.

Sailer, L.D., Gaulin, S.J.C., Boster, J.S. & Kurland, J.A. (1985) Measuring the relationship between dietary quality and body size in primates. Primates 26: 14-27.

Saint Aubin, G. de (1963) La Foret du Gabon. Centre Technique Forestier Tropical, Nogent-sur-Marne, France.

Savage, T.S. & Wyman, J. (1847) Notice on the external characters and habits of Troglodytes gorilla, a new species of orang from the Gaboon river; osteology of the same. Boston Journal of Natural History 5: 417-443.

Schaller, G.B. (1963) The Mountain Gorilla: Ecology & Behaviour. University of Chicago Press, Chicago.

Shea, B.T. (1983) Size and diet in the evolution of African ape craniodental form. Folia Primatogica 40: 32-68.

Short, R.V. (1980) The great apes of Africa. In: Short, R.V. & Wier, B.J. (eds.) The Great Apes of Africa, Journal of Reproduction & Fertility Supplement No. 28, Cambridge, pp.3-11.

Short, R.V. & Wier, B.J. (1980) The Great Apes of Africa, Journal of Reproduction & Fertility Supplement No. 28, Cambridge.

Skinner, M.F. (1986) Enamel hypoplasia in sympatric chimpanzee and gorilla. Human Evolution 1: 289-312.

Smythe, N. (1986) Competition and resource partitioning in the guild of neotropical terrestrial frugivorous mammals. Annual Review of Ecology & Systematics 17: 169-188.

Sourd, C. & Gautier-Hion, A. (1986) Fruit selection by a forest guenon. Journal of Animal Ecology 55: 235-244.

Stark, M.A. (1986) Analysis of five natural soil licks, Benoue National Park, Cameroon, West Africa. African Journal of Ecology 24: 181-187.

Stewart, K.J. (1977) The birth of a wild mountain gorilla (Gorilla gorilla beringei). Primates 18: 965-976.

Stewart, K.J. (1984) Parturition in wild gorillas - behaviour of mothers, neonates and others. Folia Primatologica 42: 62-69.

Struhsaker, T.T. (1975) The Red Colobus Monkey, University of Chicago Press, Chicago.

Struhsaker, T.T. (1978) Food habits of five monkey species in the Kibale Forest, Uganda. In: Chivers, D.J. & Herbert, J. (eds.) Recent Advances in Primatology Volume 1, Academic Press, London, pp.225-248.

Sugardjito, J., Boekhorst, I.J.A. te & van Hooff, J.A.R.A.M. (1987) Ecological contraints on the grouping of wild orang-utans (Pongo pygmaeus) in the Gunung Leuser National Park, Sumatra, Indonesia. International Journal of Primatology 8: 17-41.

Sugiyama, Y. & Koman, J. (1987) A preliminary list of chimpanzees' alimentation at Bossou, Guinea. Primates 28: 133-147.

Susman, R.L. (1987) Pygmy chimpanzees and common chimpanzees: models for the behavioral ecology of the earliest hominids. In: Kinzey, W.G. (ed.) The Evolution of Human Behavior: Primate Models, State University of New York Press, New York, pp.72-86.

Suzuki, A. (1969) An ecological study of chimpanzees in a savanna woodland. Primates 10: 103-148.

Swaine, M.D. & Hall, J.B. (1983) Early succession on cleared forest land in Ghana. Journal of Ecology 71: 601-627.

Takasaki, H. (1983) Seed dispersal by chimpanzees: a preliminary note. African Study Monographs 3: 105-108.

Teaford, M.F. & Walker, A.C. (1984) Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of Sivapithecus. American Journal of Physical Anthropology 64: 191-200.

Temerin, L.A., Wheatley, B.P. & Rodman, P.S. (1984) Body size and foraging in primates. In: Rodman, P.S. & Cant, J.G.H. (eds.) Adaptions for Foraging in Nonhuman Primates, Columbia University Press, New York, pp.24-248.

Tutin, C.E.G. & Fernandez, M. (1981) Census of the gorillas and chimpanzees of Gabon: final report of the initial survey zone. Unpublished report.

Tutin, C.E.G. & Fernandez, M. (1983a) Recensement des Gorilles et des Chimpanzes du Gabon, C.I.R.M.F., Franceville.

Tutin, C.E.G. & Fernandez, M. (1983b) Gorillas feeding on termites in Gabon, West Africa. Journal of Mammalogy 64: 511-513.

Tutin, C.E.G. & Fernandez, M. (1984) Nationwide census of gorilla (Gorilla gorilla gorilla) and chimpanzee (Pan troglodytes troglodytes) populations in Gabon. American Journal of Primatology 6: 313-336.

Tutin, C.E.G. & Fernandez, M. (1985) Foods consumed by symatric populations of Gorilla gorilla gorilla and Pan troglodytes troglodytes in Gabon: some preliminary data. International Journal of Primatology 6: 27-43.

Tutin, C.E.G. & Fernandez, M. (1987a) Sympatric gorillas and chimpanzees in Gabon. Anthroquest 37: 3-6.

Tutin, C.E.G. & Fernandez, M. (1987b) Gabon: a fragile sanctuary. Primate Conservation 8: 160-161.

Tuttle, R.H. (1975) Parallelism, brachiation, and hominoid phylogeny. In: Luckett, W.P. & Szalay, F.S. (eds.) Phylogeny of the Primates: a Multidisciplinary Approach, Plenum, New York.

Tuttle, R.H. & Watts, D. (1985) The positional behaviour and adaptive complexes of Pan gorilla. In: Kondo, S. (ed.) Primate Morphophysiology, Locomotor Analyses and Human Bipedalism, University of Tokyo Press, pp.261-288.

T-W-Fiennes, R.N. (1972) Primates: feeding. In: The UFAW Handbook of the Care and Management of Laboratory Animals, Universitys Federation for Animal Welfare, pp.388-394.

Urbain, A. (1940) L'habitat et les moeurs du gorille. Sciences (Paris) 35: 53-58.

Valker, A. (1931) La vie du gorille au Gabon. Bulletin du Museum National d'Histoires Naturelles 3: 393-398.

Vedder, A.L. (1984) Movement patterns of a group of free-ranging mountain gorillas (Gorilla gorilla gorilla) and their relation to food availability. American Journal of Primatology 7: 73-89.

Vedder, A. (1987) Report from the gorilla advisory committee on the status of Gorilla gorilla. Primate Conservation 8: 75-81.

Veit, P.G. (1982) Gorilla society. Natural History 91: 48-59.

Walker, A. (1981) Diet and teeth. Dietary hypotheses and human evolution. Philosophical Transactions of the Royal Society of London 292: 57-64.

Waser, P. (1975) Monthly variations in feeding and activity patterns of the mangabey, Cercocebus albigena. East African Journal of Wildlife 13: 249-263.

Waser, P. (1977) Feeding, ranging and group size in the mangabey, Cercocebus albigena. In: Clutton-Brock, T.H. (ed.) Primate Ecology, Academic Press, London, pp.183-222.

Waser, P.M. & Brown, C.H. (1986) Habitat acoustics and primate communication. American Journal of Primatology 10: 135-154.

Waser, P.M. & Floody, O. (1974) Ranging patterns of the mangabey, Cercocebus albigena, in the Kibale Forest, Uganda. Zeitschrift fuer Tierspsychologie 35: 85-101.

Waterman, P.G. (1984) Food acquisition and processing as a function of chemistry. In: Chivers, D.J., Wood, B.A. & Bilsborough, A. (eds.) Food Acquisition & Processing in Primates. Plenum Press, London, pp.177-211.

Waterman, P.G., Choo, G.M., Vedder, A.L. & Watts, D.P. (1983) Digestability, digestion-inhibitors and nutrients of herbaceous foliage and green stems from an African montane flora and comparison with other tropical flora. Oecologia 60: 244-249.

Watts, D.P. (1983) Foraging strategy and socioecology of mountain gorillas (Pan gorilla beringei). PhD Thesis, University of Chigago.

Watts, D.P. (1984) Composition and variability of mountain gorilla diets in the Central Virungas. American Journal of Primatology 7: 323-356.

Watts, D.P. (1985) Relationships between group size and composition and feeding competition in mountain gorilla groups. Animal Behaviour 33: 72-85.

Watts, D.P. (1987) Effects of mountain gorilla foraging activities on the productivity of their food plant species. African Journal of Ecology 25: pp.155-163.

Webb, L.J., Tracey, J.G., Williams, W.T. & Lance, G.N. (1967) Studies in the numerical analysis of complex rain-forest communities. II. The problem of species-sampling. Journal of Ecology 55: 525-538.

Weber, A.W. & Vedder, A.L. (1983) Population dynamics of the Virunga gorillas 1959-1978. Biological Conservation 26: 341-366.

Wheatley, B.P. (1987) The evolution of large body size in orangutans: a model for hominoid divergence. American Journal of Primatology 13: 313-324.

Wheelright, N.T. (1985) Competition for dispersers and the timing of flowering and fruiting in a guild of tropical trees. Oikos 44: 465-477.

Whitesides, G.H. (1985) Nut cracking by wild chimpanzees in Sierra Leone, West Africa. Primates 26: 91-94.

Whitmore, T.C. (1978) Gaps in the canopy. In: Tomlinson, P.B & Zimmerman, M.H. (eds.) Tropical Trees as Living Systems, Cambridge University Press, Cambridge, pp.639-656.

Whitmore, T.C. (1984) Variation within tropical lowland evergreen rain forest and its causes. In: Tropical Rain Forests of the Far East, 2nd Edition, Clarendon Press, Oxford, pp.217-242.

Whitmore, T.C., Peralta, R. & Brown, K. (1985) Total species count in a Costa Rican tropical rain forest. Journal of Tropical Ecology 1: 375-378.

Whitten, A.J. (1982) A numerical analysis of tropical rain forest using floristic and structural data and its application to an analysis of gibbon ranging behaviour. Journal of Ecology 70: 249-271.

Williamson, E.A., Tutin, C.E.G. & Fernandez, M. (1988) Western lowland gorillas feeding in streams and on savannas. Primate Report 19: 29-34.

Wilson, C.C. & Wilson, W.L. (1975) The influence of selective logging on primates and some other animals in East Kalimantan. Folia Primatologica 23: 245-274.

Wing, L.D. & Buss, I.O. (1970) Elephants and forests. Wildlife Monographs 19: 1-92.

Wrangham, R.W. (1974) Artificial feeding of chimpanzees and baboons in their natural habit. Animal Behaviour 22: 83-93.

Wrangham, R.W. (1975) The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. PhD Thesis, University of Cambridge.

Wrangham, R.W. (1977) Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock, T.H. (ed.) Primate Ecology, Academic Press, London pp.503-538.

Wrangham, R.W. (1979) On the evolution of ape social systems. Social Science Information 18: 335-368.

Wrangham, R.W. (1986) Ecology and social relationships in two species of chimpanzee. In: Rubenstein, D.I. & Wrangham, R.W. (eds.) Ecological Aspects of Social Evolution. Birds & Mammals, Princeton, New Jersey, pp.352-378.

Yamagiwa, J. (1983) Diachronic changes in two eastern lowland gorilla groups (Gorilla gorilla graueri) in the Mt. Kahuzi Region, Zaire. Primates 24: 174-183.

Yamagiwa, J. (1986) Activity rhythm and the ranging of a solitary male mountain gorilla (Gorilla gorilla beringei). Primates 27: 273-282.

Yamagiwa, J. (1987) Intra- and inter-group interactions of an all-male group of Virunga mountain gorillas (Gorilla gorilla beringei). Primates 28: 1-30.

Yerkes, R.M. (1951) Gorilla census and study. Journal of Mammalogy 32: 429-436.

Yerkes, R.M. & Yerkes, A.D. (1929) The Great Apes, Yale University Press, New Haven.